HABITAT AND ECOLOGY OF BREEDING AND NON-BREEDING WHITE-TAILED TROPICBIRDS (*PHAETHON LEPTURUS CATESBYI*) IN BERMUDA

By

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ABSTRACT

Pelagic seabirds have terrestrial and marine life stages and conditions at both sites can affect survival. On land, seabirds are threatened by destruction of nests and introduced predators. Assessments of threats at-sea, however, requires data on pelagic movement and behaviour, which is unknown for many seabirds. To mitigate degradation of breeding sites, artificial cavities are sometimes used. To identify pelagic activities geolocators (GLS) are a useful tool. However, data on nest-site selection, nest success and predation of artificial and natural seabird cavities are limited. In Bermuda, we monitored 158 natural and 178 artificial cavities of White-tailed Tropicbirds (*Phaethon lepturus catesbyi*) in 2013-2015. Tropicbirds favoured natural cavities with nesting sand, smaller entrances and on steeper cliffs. Artificial cavity occupancy varied by location, year and cavity depth. Clutch survival increased in deeper cavities, with smaller entrances and no rubble. Nestling survival varied by year and increased with age. American Crow (*Corvus brachyrhynchos*) predation was higher in natural cavities, and shallower cavities with larger entrances. We obtained GLS data from 25 recaptured tropicbirds in 2015 and learned that birds in the fall and winter ranged from Bermuda to the Mid-Atlantic Ridge. Non-breeders spent 95% of night periods and 59% of day periods wet. We found nest-cavity traits and temporal factors important for nesting tropicbirds. However, introduced rats were unaffected by cavity dimensions and should be removed. Lastly, we found, for the first time, marine areas where Atlantic tropicbirds are vulnerable and can be studied for pelagic threats.

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1. Introduction and Overview

1.1 Thesis Background

Seabird Ecology

Seabirds represent a large and diverse group of birds that evolved to exploit and thrive in a pelagic habitat (Ashmole 1971). Approximately 345 species (3.5% of all bird species) of seabirds have been identified (Croxall et al. 2012). What defines a seabird is not always clear because different species vary greatly in time spent using terrestrial and marine habitats. For example, some seabirds are more coastal, foraging no further than 5 km from land and remaining on land even during the non-breeding period (Dunnet et al. 1990, Shealer 2002). Examples of coastal seabirds include many species of gulls and terns (Laridae). On the other hand, other species are more pelagic, coming to land only to breed, and spending their entire non-breeding period on the open ocean (Dunnet et al. 1990, Guilford et al. 2009). Examples of pelagic seabirds include petrels and albatrosses (Procellariiformes).

The nesting ecology of pelagic seabirds, one of two themes of this thesis, is well studied. Researchers have found specific traits are common among breeding pelagic seabirds: (1) single egg clutches, (2), long nesting periods, (3) delayed maturity and (4) long lifespans (Ricklefs 1990). Remote oceanic islands often serve as nesting habitat for pelagic seabird colonies (Brown et al. 1990).

Seabird threats relating to human settlement

It's hypothesized that remote oceanic island nesting evolved as an antipredator response, due to the absence of mammalian predators (Lack 1968, Brown et al. 1990). Although nesting seabirds were initially free of mammalian predators on remote islands, this prolonged separation eventually caused the loss of antipredator behaviour (Kepler 1967, Moors and Atkinson 1984, Beauchamp 2004). As a consequence, the colonization of remote islands by humans, dating back to 1000 years b.p., had disastrous consequences for breeding seabird bird populations (McGlone 1989, Wingate 1990, Monteiro et al 1996, Convey and Lebouvier 2009, Cheke 2010). Specific mammalian predators that accompanied humans to remote islands include rats (*Rattus spp.*; Jones et al. 2008), cats (*Felis catus*; Ratcliffe et al. 2010), dogs (*Canis familiaris*; McChesney et al. 1998), pigs (*Sus scrofa*; Challies 1975) and foxes (*Vulpes*; Maron et al. 2006). Out of these, rats and cats inhabit 80% and 65% of major island systems respectively, making them the primary predators of nesting seabirds (Atkinson 1985, 1989, Jones et al. 2008).

Introduced rats prey on seabird eggs, chicks and adults and have caused the extirpation of at least 4 storm petrel species (Hydrobatidate) from oceanic islands across all oceans (Atkinson 1985, Jones et al. 2008). Similarly, introduced cats have caused the supposed extinction of the endemic Guadalupe Storm-Petrel (*Oceanodroma macrodactyla*), and decimated breeding pairs of Grey-faced (*Pterodroma gouldi*), Black (*Procellaria parkinsoni*) and Cook's Petrel (*Pterodroma cookii*) breeding on Little Barrier Island, New Zealand (Jehl 1972, Imber 1975). A

study on Marion Island estimated that one cat killed approximately 213 burrowing petrels a year in order to meet energetic requirements (van Aarde 1980).

Humans also have had direct negative effects on nesting seabirds through intensive hunting and consumption, contributing to seabird extirpation. For example, in Hawaii, numerous seabird bones, including the Hawaiian Petrel (*Pterodroma sandwichensis*), left by native Hawaiians, have been found scattered across the island in areas where the bird no longer breeds (Olson and James 1982). Similarly, researchers discovered the subfossil remains of the Bermuda Petrel (*Pterodroma cahow*), a previously superabundant seabird across the island, but today consisting of approximately 100 breeding pairs on five small, offshore islets (Carlile et al. 2012). Additional threats came from severe habitat modification on remote islands, disrupting breeding. For example, in New Zealand, large areas of forest were removed through burning and subsequently replaced with nutrient poor green space and shrubs, presumably making burrow construction difficult for breeders (McGlone 1989). Similarly, the arrival of the Polynesians to Magana (Cook Islands) lead to severe soil erosion among seabird nesting habitat (Kirch 1991).

Conservation of cavity-nesting seabirds

In addition to international agreements to conserve all biodiversity (e.g., The Convention on Biological Diversity), conservationists argue that the preservation of seabirds is important. Firstly, their abundance across the world's oceans allow researchers to assess direct and indirect impacts of ocean pollutants, including oil and

mercury (Furness and Camphuysen 1997). Secondly, seabird abundance can be used to assess abundance and availability of marine food supplies the ocean (Piatt et al. 2007, Parsons et al. 2008). Additional conservationists estimate that almost one-third of all seabird species are threatened with extinction and are more threatened than any other avian group of similar size (Croxall et al. 2012). In particular the order Procellariiformes, comprised largely of burrow- and cavity-nesting seabirds, in particular, is declining faster than any other avian order (IUCN 2010, Croxall et al. 2012).

The earliest conservation efforts geared towards cavity-nesting seabirds dates back to the 1960s and 1970s (Wingate 1977, Byrd et al. 1983). The primary objective of these management projects was the restoration of breeding populations to numbers that were estimated to be present prior to human settlement. The specific strategies implemented varies greatly, depending on colony-specific threats. In colonies where nest sites are severely limited, mass installation of artificial nest-cavities may be implemented.

Artificial nest-cavities have been used to offset decline in many cavity-nesting seabirds, like the Bermuda Petrel, Gould's Petrel (*Pterodroma leucoptera*; Priddel et al. 2006), Fluttering Shearwater (*Puffinus gavia*; Miskelly et al. 2009) and Hutton's Shearwater (*Puffinus huttoni;* Miskelly et al. 2009). Artificial cavities in these conservation studies were used in the translocation of fledglings, which if timed correctly, encourages fledglings to return to these sites as prospecting adults (Carlile et al. 2012). Although beneficial, the translocation of fledglings from natural to artificial

nest-cavities can be problematic. For example, if artificial nest-dimensions are not correct, departing chicks may become wedged in entrances and die (Miskelly et al. 2009). Secondly, translocated chicks may successfully fledge from artificial nest-cavities made of stone or plastic, but returning, translocated birds may only return to the stone burrows (Madeiros pers. comm.)

A well-recognized concept that is intimately linked to the breeding area occupied by cavity-nesting seabirds is nest-site selection. Nest-site selection is the study of specific variables, usually related to the nest-site or nest-cavity, which can potentially explain the occupancy of that space by a breeding species (Clark et al. 1983). Unlike the translocation examples, birds in nest-site selection studies are free to choose nest-cavities. For the remainder of this thesis, I will use the term "nest-site selection" to refer to the occupancy of a nest-cavity. Previous studies suggest multiple nest-cavity variables believed to determine cavity occupancy: nest-cavity location (Ambrose 1982), cavity depth (Belthoff and Ritchison 1990), entrance height (Menkhorst 1984), entrance hole orientation (Hooge et al. 1999) and temperature (Ardia et al. 2006). These factors have been rigorously tested with terrestrial avian cavity-nesting families, including falcons (Negro and Hiraldo 1993), woodpeckers (Pasinelli 2007), tits (Nilsson 1984) swallows (Rendell and Raleigh 1989), parrots (Olah et al. 2014) and owls (Belthoff and Ritchison 1990).

Nest-site selection in cavity-nesting seabirds

One of the pioneer, and highly cited studies on nesting seabirds is the investigation of cavity occupancy as a function of cavity depth, entrance height, neighbor numbers, vegetation cover, shelter and orientation among four members of the procellariiform group (Ramos et al. 1997). Two later studies investigated nest-cavity selection in the Yelkouan Shearwater (*Puffinus yelkouann*), concluding these birds preferred natural cavities at lower elevation, that were deeper, containing a winding tunnel and reduced vegetation cover near entrance (Bourgeois and Vidal 2007, Bourgeois et al. 2014).

There is also some published work on the occupancy rates of artificial cavities used by nesting seabirds. For example, a study on nesting European Storm-Petrels (*Hydrobates pelagicus*) found a gradual increase in occupancy of artificial cavities across a five year period following installation (De León and Mínguez 2003). Surprisingly, only two out of the 43 artificial cavities at the largest storm petrel colony were used for duration of the five year study period. A similar study reported a maximum occupancy of 19% out of 115 artificial boxes installed for Madeiran Storm-Petrels (*Oceanodroma castro*) (Bolton et al. 2004). In contrast, some studies report high occupancy of artificial cavities, as seen with the Little Penguin (*Eudyptula minor*; Sutherland et al. 2014)

The above research on nest-cavity selection among natural seabird cavities has created additional avenues for future research. The chosen explanatory variables for natural cavity occupancy are reasonable to collect and have increased our

understanding of these seabird species. Unfortunately, compared to similar work on terrestrial, avian cavity nesters, there are far fewer examples of nest-cavity selection studies for seabirds. Out of the few that that exist, most involve procellariiform seabirds because of their burrow and cavity-nesting behaviour. Considering the relatively large number of seabirds that use rocky cavities, including seabirds that normally dig and nest in soil burrows, it is difficult to generalize these findings across all cavity-nesting seabird taxa. Therefore, there is a pressing need to repeat similar nest-selection studies on other cavity nesting seabirds, in order to further our understanding of cavity-nesting seabird biology.

The same can be argued for seabirds that also have the option of nesting in artificial nest-cavities, with selection studies in these nest-cavities also being scarce in the ornithological literature. The above research undoubtedly highlights the enormous potential artificial cavities have for breeding seabirds. However, the mixed findings of low and high occupancy of artificial cavities suggests that their might also be nest-site selection patterns at work. Therefore, in order to further understand potential determinants of artificial cavity occupancy, the techniques provided by the other seabird biologists who investigated natural cavities need to be applied to artificial cavities.

Nest success in cavity-nesting seabirds

Nest-site selection is intimately linked to the survival and persistence of cavity-nesting seabirds. More specifically, poor nest sites can leave breeders vulnerable to flooding

(Thompsoan et al. 1991), density-dependent predation (Stokes and Boersma 2000), difficulty arriving at and departing from nest sites (Catry et al. 2009) and increased competition (Wallace et al. 1992). The limited research on nesting success in cavity-nesting seabirds has suggested that breeders inside natural cavities showed higher success in deeper cavities, with winding tunnels, larger entrance heights, higher block covers and less rubble within nesting sand (Ramos et al. 1997, Bourgeois and Vidal 2007, Bourgeois et al. 2014). Similarly, seabirds in artificial cavities have been found to have higher breeding survival, compared to those nesting in natural cavities, including Rhinoceros Auklet (*Cerorhinca monocerata*), European Storm-Petrel, Madeiran Storm-Petrel and Wedged-tailed Shearwater (*Ardenna pacificus*) (Byrd et al. 1983, de León and Mínguez 2003, Bolton et al. 2004).

The previous nest success studies on breeding seabirds in natural cavities strengthens the idea that nest-cavity choice is non-random and birds actively seek nest-sites that improve breeding success. Despite these clear and important implications for nesting seabirds, two (Bourgeois and Vidal 2007, Bourgeois et al. 2014) out of three of those studies were based solely on the Yelkouan Shearwater. Nest success studies on other cavity nesting seabirds appears to be limited, unlike the exhaustive list of such work on terrestrial cavity nesters (Negro and Hiraldo 1993, Klein et al. 2007). Once again, it is challenging to apply the trends seen with so few cavity-nesting seabirds to the many that exist. With this realization in mind, and the important implications for seabirds using artificial nest-cavities, further nest success

research on another cavity-nesting seabird species is important to increase our understanding.

Introduced mammalian and avian predators of cavity-nesting seabirds

Introduced rats threaten breeding seabirds on remote oceanic islands because they can prey on any life stage (Atkinson 1985). The vulnerability of ground-nesting seabirds to rat predation has been well documented (Kepler 1967, Taylor 1979, Jones et al. 2005). In contrast, fewer studies have investigated the relationship of specific nest cavity traits and vulnerability to rat predation. One of the few that does exist found that nesting Yelkouan Shearwaters typically selected the deepest and most winding natural cavities, which were seldom visited by introduced rats (Ruffino et al. 2008). These results appear to be the first to suggest that cavity complexity has significant implications on rat visitations and in turn, predation. In contrast, Black Rats (*Rattus rattus*) on Langara Island readily entered Ancient Murrlet (*Synthliboramphus antiquus*) burrows and preyed on adults, seemingly irrespective of burrow characteristics (Bertram 1995). In addition to natural cavities, some seabirds have been provided with artificial cavities, with some being prone to rat predation. For example, cavity-nesting Scripps's Murrelet (*Synthliboramphus scrippsi*) experienced rat predation among artificial nests (Jones et al. 2005).

Avian predators also pose a threat to cavity-nesting seabirds. For example, the Common Raven (*Corvus corax*) and Yellow-legged Gull (*Larus michahellis*) are

predators of Xantus's Murrelet (*Synthliboramphus hypoleucus scrippsi*) and the European Storm-Petrel respectively (De León and Mínguez 2003, Jones et al. 2005, Sanz-Aguilar et al. 2009). Interestingly, the artificial European Storm-Petrel cavities were less prone to Yellow-legged Gull predation, compared to natural cavities (De León and Mínguez 2003). Despite these important findings, it is noteworthy that the Common Raven and Yellow-legged Gull are both native avian predators to their respective ranges, whereas specific examples of the impact an introduced avian predator have on cavity-nesting seabirds is largely unknown.

The research above highlights the accessibility of seabird nest-cavities to mammalian and avian predators. The next step is to fill in the gaps in our knowledge about which specific nest-cavity characteristics are likely to explain their vulnerability. This is especially true for introduced avian predators, with current research apparently limited to the examples discussed above. Researchers can expand on current knowledge on this matter by investigating specific nest-cavity characteristics of an entirely different cavity-nesting seabird. Furthermore, such knowledge will have important implications for artificial cavities, which have become an important conservation tool, particularly with the translocation of seabird fledglings (Miskelly et al. 2009).

1.2 Non-breeding distribution of seabirds

What we currently know about post-breeding seabird movement

Unlike their breeding ecology, the wintering whereabouts of most pelagic seabirds remains largely unknown. During breeding, seabirds spend a larger proportion of time on land, allowing intimate observations, whereas non-breeding pelagic seabirds disperse widely across the ocean, rendering them inaccessible (Votier et al. 2011). The non-breeding period is also when seabird mortality can be at its highest because of harsh weather conditions, shortened day length, which limits foraging time, reduced concentrations of prey and exposure to oil spills (Harris and Wanless 1994, Votier et al. 2005, Daunt et al. 2006, Harris et al 2007). During the non-breeding period, some seabirds may disperse thousands of kilometers from their breeding grounds. For example, non-breeding Sooty Shearwaters (*Ardenna griseus*) depart breeding sites in southern South America and New Zealand and migrate to wintering areas in the Northern Atlantic and Pacific Oceans (Phillips 1963, Hedd et al. 2014). Seabird migration is also driven by both prey availability and weather (Tasker et al. 1985, Dingle 1996, Fredriksen et al. 2004).

Although some adult seabirds return to breed annually, like Common Terns (*Sterna hirundo*; Nisbet et al. 2011) and Razorbills (*Alca torda*; Lloyd and Perrins 1977) other species can skip breeding for a year (i.e., "sabbatical"), like Blue Petrel (*Halobaena caerulea*; Chastel et al. 1995) Snow Petrel (*Pagodroma nivea*; Angelier et al. 2009) and Wandering Albatross (*Diomedea exulans*; Weimerskirch et al. 2015),

and remain at-sea. Juvenile seabirds can spend 2-10 consecutive years at sea, before returning to breeding sites for the first time (Van Ryzin et al. 1976, Nisbet et al. 1984, Angelier et al. 2007). These long periods at sea leave seabirds prone to multiple threats, including long-line fishing, oil spills, pollutants from offshore drilling, interactions with offshore hydrocarbon platforms, attraction to artificial night-lighting at sea and incineration from oil and gas-based platforms (Wiese et al. 2001, Montevecchi 2006, Anderson et al. 2011, Burke et al. 2012, Ronconi et al. 2015). The ever growing list of threats faced by pelagic seabirds places great urgency in identifying their pelagic distribution.

Techniques used to study movement of non-breeding seabirds

The 1920s marked the earliest known studies of pelagic seabird movement through at-sea ship surveys (Jespersen 1924). Ship surveys involves conducting a census of seabird richness and abundance, usually within a predefined boundary. Although seemingly simplistic, the methodology of at-sea ship surveys have undergone enormous revisions and refinement to correct for large errors and biases (Tasker et al. 1984, Barbraud and Thiebot 2009).

The most widely accepted approach is ship strip transects, which assumes all seabirds within proximity to the strip transect are seen and the specified width of the strip is maintained during all trials (van Franeker 1994). However, ship surveys contain inherent flaws that reduce the accuracy of seabird abundance and distribution.

For example, larger species are more likely to be detected, compared to smaller species. Gregarious species, like murres (*Uria* spp.), are more likely to be observed compared to solitary species like puffins (*Fratercula* spp.) (Tasker et al. 1984). Seabirds also respond differently to the presence of ships, with some species being ship-followers, such as gulls (Laridae) or avoiders, such as loons (Gavvidae). (Briggs et al. 1985). Detection of seabirds also depends largely on weather conditions and individual observer detection ability (Dixon 1977, Ronconi and Burger 2009). Lastly, at-sea ship surveys give no information on colony origin of observed individuals and are limited to small search areas.

Ring and recapture studies, when researchers fit individuals with a unique identification leg-ring prior to release, have increased our understanding of the pelagic distribution of seabirds (Perrins 1976, Morant et al. 1983). Mass ringing and recapture of seabirds has been practiced for decades, with 58 species already been ringed in Canada, as of 1995 (Gaston et al. 2008). The intent is to gain information from re-sighted or recaptured birds in distant localities, as seen with 23 species of ringed seabird species that were captured elsewhere (Olmos 2013). Despite these benefits, this approach has several shortcomings. First, to be effective, it requires the mass ringing of the targeted population to offset the low ring-recoveries commonly reported (Weimerskirch et al. 1985, Croxall and Prince 1990). Second, the location where a ringed-carcass are recovered may not necessarily represent where the individual died and may distort the actual non-breeding range. This is especially true if the bird died

at sea and its carcass drifted considerable distances by currents (Bibby and Lloyd 1977, Wiese and Robertson 2004).

The past few decades have marked an influx of innovative technology allowing ornithologists to track the annual movements of migratory seabirds. One of the earliest uses of advanced technology for avian tracking was accomplished with 180 gram satellite transmitters fitted on the Wandering Albatross (*Diomedea exulans*), where individuals travelled an estimated 3,600-15,000 km during a single foraging trip (Jouventin and Weimerskirch 1990). Satellite transmitters, with a reported accuracy 100 meters to 50 km, have tracked the non-breeding movements of migratory seabirds, while simultaneously providing support for the creation of marine protected areas used by some taxa, like Black-browed (*Thalassarche melanophrys*) and Grey-headed Albatrosses (*T. chrysostoma*) (Terauds et al. 2006).

In addition to precise accuracy, satellite tags transmit daily fixes of the tracked animal, without needing to recapture the individual. Previously, satellite tags were restricted to a small number seabird taxa because the smallest units were ~22 grams (Bridge et al. 2011). Experts suggest devices should weigh ~ 3-5% of the model specie's mass (Barron et al. 2010). This means 22 gram GPS satellite tags are limited to birds weighing about 450 grams, ~14% species of all avian species. (Bridge et al. 2011). Devices conforming to the "3% rule," however, may still hinder flight of carriers via drag, emphasizing the need for careful concern of targeted species and device choice (Vandenabeele et al. 2011). Although smaller satellite tags, weighing 1.6 grams, recently became available on the market, these devices are still extremely

expensive and have a relatively short lifespan due to battery requirements (N. Clark unpubl. data, Bridge et al. 2011). Smaller archival GPS tags, which share the same accuracy and high energy expenditures of larger satellite tags, are another option for tracking seabirds. However, even the relatively light mass (5 grams) of the current smallest GPS archival tag are limited to approximately half of all avian species (Bridge et al. 2011).

A relatively inexpensive tracking device suited for mapping pelagic movements of seabirds are light-based geolocators (or GLS tags). GLS tags weigh 0.5-1 grams, making them applicable to most avian species (Bridge et al. 2011). However, they have some shortcomings. For example, latitude and longitude are derived from day length (i.e. sunrise to sunset) and local noon time respectively, producing a mean error ± SD of 186 ± 114 km (Phillips et al. 2004a). Their reliance on light makes calculating daily positions problematic during equinox periods, where day length does not vary across latitude (Nielsen et al. 2006). Nevertheless, several analytical techniques have been applied to GLS data to reduce this error, producing reliable estimates of large scale movement (Phillips et al. 2004a).

Researchers have used GLS tags to track the movements of smaller pelagic taxa. These studies have discovered staggering movement patterns, filling knowledge gaps in migration ecology. For example, GLS tracking revealed that Arctic Terns (*Sterna paradisaea*) travel 80,000 km between their northern Arctic breeding grounds and southern Antarctic wintering grounds, revealing the longest migration of any animal on the planet (Egevang et al. 2010). A similar GLS study on the small Cook's Petrel

revealed that two distinct populations from New Zealand showed transequatorial separation of non-breeding areas (Rayner et al. 2011).

In addition to revealing novel seabird distributions, GLS application have also had enormous conservation implications. More specifically, Flesh-footed Shearwaters (*Ardenna carneipes*) from Lord Howe Island, which supports the largest number of this species, were shown to winter in the Yellow and East China Seas, where longline fishing is heavily practiced (Reid et al. 2013). Similarly, the wintering range of Thick-billed Murres (*Uria lomvia*) from Nunavut overlaps with oil production zones in the Grand Banks of Newfoundland (Tranquilla et al. 2013).

GLS loggers can also be used to identify potential sexual segregation in migratory seabirds. Pelagic sexual segregation occurs when sexes exploit different waters during the breeding and non-breeding seasons (González-Solís et al. 2000, Åkesson and Weimerskirch 2014). Some explanations are related to specific differences between sexes, which include size dimorphism (Phillips et al. 2004b) and different wing morphologies, which are more effective in some pelagic areas over others (Navarro et al. 2009). For example, seabirds with higher wing loading (i.e., weight per area of lift) can effectively exploit pelagic areas with stronger winds, compared to seabirds with smaller wing loading (Suryan et al. 2008). Regardless of the mechanism, understanding if males and females differ in pelagic distribution is important because one sex may be more vulnerable to threats than the other, depending on areas exploited. However, most studies on sexual segregation have focused on larger seabirds, such as albatrosses, shearwaters and penguins during the breeding season

(González-Solís et al. 2000, Phillips et al. 2005, Thiebot et al. 2011, Hedd et al. 2014). GLS tags allow researchers to look for such patterns with smaller seabird species.

Some light-based geolocators can also record periods of salt water immersion and dryness, allowing pelagic activities to be quantified. More specifically, geolocators can give new insights into the day and night activities of pelagic seabirds. Mackley et al. (2010) performed a comparative analysis on the pelagic activities of four albatross species, with geolocator immersion data indicating post-breeding birds spent more time flying during the day than night, despite all birds being predominantly wet during the day.

Similar immersion data revealed, for the first time, that island populations of the Brown Skua (*Stercorarius antarcticus*) were also more active during the day compared to night (Phillips et al. 2007). In contrast, tagged White-chinned Petrels (*Procellaria aequinoctialis*) and Bulwer's Petrel (*Bulweria bulwerii*) exhibited higher nocturnal activity (Mackley et al. 2011, Dias et al. 2015). Differences in day and night activities among seabird species reflect differences in seabird foraging, with day flight indicative of seabirds hunting schooling fish on the surface during the day and night flight representing seabirds foraging for mesopelagic fishes and squids that migrate to the surface at night (Kozlov 1995). Thus, geolocators provide researchers with novel techniques to thoroughly investigate this largely unknown aspect of natural history of migratory, pelagic seabirds.

1.3 Thesis hypotheses for nest-site selection, nest success and predation

The first half of this thesis will address nest-site selection, nesting success and predation of cavity-nesting seabirds, using natural and artificial cavities. Previous studies focused largely on nest-site selection and success of natural cavities, whereas research on such factors with respect to artificial cavities are limited. Similarly, studies investigating specific nest-site characteristics that could explain their vulnerability to rats and introduced avian predators are very limited. These knowledge gaps lead to some interesting questions. First, what are the nest-cavity characteristics of the more frequently used natural and artificial cavities occupied by nesting seabirds? Second, are some of these nest-cavity characteristics associated with nest success? Third, do certain nest-cavity characteristics reduce the accessibility of nests to introduced mammalian and avian predators?

I studied the breeding population of cavity-nesting White-tailed Tropicbirds (*Phaethon lepturus catesbyi*) in Bermuda to address the above research questions. More specifically, I will test nest-site selection, nesting success and predation from introduced predators using the following specific variables: cavity type (natural or artificial), cavity location (mainland or offshore island), nesting substrate (absent or present), rubble in nesting sand (absent or present), year (2013, 2014 and 2015) cavity depth, entrance height, coastal slope and neighbor numbers.

I hypothesized that natural cavity occupancy is influenced by cavity location, presence of nesting sand, year, cavity depth, entrance height and coastal slope.

Similarly, location, year and nest depth were hypothesized to be important predictors of artificial cavity occupancy. The remaining variables were not considered among our artificial cavities because these cavities all had nesting sand, similar entrance heights and were all installed on steep cliffs. I predicted higher occupancy of natural and artificial cavities on offshore islands, compared to mainland sites, because the former breeding sites has undeveloped coastal, breeding habitat and less mammalian predators than cavities on the latter sites. I also expected natural cavities lined with nesting sand to have higher occupancy than natural cavities without nesting sand because the sand may protect eggs from the jagged limestone flooring, thereby reducing the risk of egg breakage during incubation. I considered their might be annual variations in occupancy of natural and artificial cavities across years because of inherent variability between nesting seasons. I predicted deeper natural and artificial cavities would have higher occupancy because deeper cavities may be less vulnerable to predation from introduced and rats and American Crows (*Corvus branchyrhynchos*). I expected natural cavities with smaller entrances to be favoured, compared to natural cavities with larger entrances because smaller entrances may limit access to rats and crows. Lastly, I predicted natural cavities located on steeper cliffs to have higher occupancy than those on flatter coastal terrain because nest-cavities on steeper cliffs may be harder for rats to reach.

For this thesis, nest success was divided into clutch and nestling survival of White-tailed Tropicbirds. I hypothesized that clutch survival depended on cavity type, cavity location, rubble in nesting sand, year, cavity depth, entrance height, coastal slope and

neighbor numbers. I expected clutch survival to be higher in artificial cavities than natural cavities because artificial cavities have smaller entrances and are located along steeper cliffs, both factors expected to limit rat predation. In contrast I predicted that crows would be limited solely by smaller entrance heights and not coastal slope because of their ability to fly. I predicted clutch survival would be higher on island sites compared to mainland sites because rats are less abundant on island sites, compared to mainland sites. Nest-cavities containing rubble in nesting sand were predicted to have lower clutch survival than cavities without rubble because stones can damage eggs during incubation. I predicted clutch survival to vary across the three year study period because rat and crow predation could have varied during this study period. I predicted that clutches inside deeper cavities, with smaller entrances and on steeper cliffs would have higher clutch survival than shallower cavities, with larger entrances and on flatter terrain because cavities with the former traits would be harder for rats to reach. I expected crows to only be limited by cavity depth and entrance height. Lastly, I predicted clutch survival to be lower in nest-cavities with many neighbors, compared to nest-cavities with fewer neighbors, because predators may me more likely find nest sites with more neighbors.

Similarly, I hypothesized nestling survival to be influenced by cavity type, cavity location, year, cavity depth, entrance height, coastal slope, neighbor numbers, day of the year and nestling age. I predicted nestling survival to be higher in artificial cavities, compared to natural cavities, because artificial cavities have smaller entrances and installed on steeper cliffs, which might limit access to rats, whereas

crows would be restricted by the entrance height. Nestling survival was expected to be higher on the island sites, compared to mainland sites, because the island sites have fewer rats than the mainland sites. I predicted nestling survival to vary across the three year study period because rat and crow predation could vary by year. Nestlings were predicted to survive better in deeper cavities, with smaller entrances and located on steeper cliffs, compared to shallower cavities with larger entrances and on flatter coastal terrain because nest-cavities with the former traits might be harder for rats to reach; whereas crows are expected to be limited only by cavity depth and entrance height. Nestling survival was predicted to be lower in nest-cavities with many neighbors because rats and crows may be more likely to find nest sites in high densities, compared to those with fewer neighbors. I expected nestling survival to be higher during the later portion of the breeding season, compared to early in the season, because nestling predation may be higher when nesting colonies are at their densest, compared to later in the season when most breeders have left Bermuda. Lastly, I predicted nestling survival to increase with nestling age because younger chicks may be more vulnerable to rat and crow predation, than older chicks.

I hypothesized that rat predation would be affected by cavity type, cavity location, year, cavity depth, entrance height, coastal slope and neighbor numbers. Crow predation was hypothesized to be affected by all of these variables, except for location and coastal slope, because all recorded crow predation occurred on island sites and coastal slope was assumed not to affect crow predation due to their flight. I predicted higher rat and crow predation in natural cavities, compared to artificial cavities,

because artificial cavities have smaller entrances that might limit access to rats and crows. Rat predation was predicted to be higher on the mainland sites, compared to island sites, because rats were more abundant on the mainland. I predicted rat predation to vary across the three year study period because rat abundance across sites may vary by year. I expected crow predation to decrease with year because crow culling efforts were enforced during the last two years of the study. I predicted rat and crow predation to be lower in deeper cavities with smaller entrances, compared to shallower cavities with larger entrances because cavities with the former characteristics may be less vulnerable to rats and crows. I predicted nest-cavities on stepper cliffs would be less vulnerable to rat predation than cavities on flatter terrain because rats may have difficulty reaching nest-cavities on stepper cliffs. Finally, I predicted that rat and crow predation would be higher among nest-cavities with more neighbors than nest-cavities with fewer neighbors because these predators could be attracted to the higher concentration of birds.

1.4 Thesis objectives and predictions for post-breeding distribution and at-sea activities of seabirds

For the second half of this thesis, I used small, light-based geolocators to identify the non-breeding distribution and pelagic activities of a tropicbird species. Despite many publications on seabird migration using GLS tags, knowledge about the non-breeding distribution and behaviour of tropicbirds remains limited. Currently, only two such studies exist for tropicbirds. The first used radio telemetry to follow White-tailed

Tropicbirds 89 km from Puerto Rico (Pennycuick et al. 1990). However, observations were based on two birds, whose tracks were followed for a few days. The second study used light-based geolocators to identify the non-breeding distribution of White and Red-tailed Tropicbirds (*Phaethon rubricauda*) from Cousin, Europa and Madagascar in the Indian Ocean (Le Corre et al. 2012). However, the tropicbird movements were described in limited detail because the study focused on an additional five species.

Current understanding of the pelagic movements of tropicbirds are based largely on at-sea ship surveys. In the Indian Ocean, White and Red-tailed Tropicbirds were seen 1,300 km and 120 km respectively from the nearest known breeding colony on Christmas Island (Dunlop et al. 1988). Within the Pacific Ocean, Red-tailed Tropicbirds have been seen northwest in Japan (39°N; Austin and Kuroda 1953); Mexico (20°N, 106°45′W, 113 km from shore), and California (Spear and Ainley 2005). However, these vessel sightings provide limited information on colony origin and virtually no information on whether tropicbirds exhibit at-sea sexual segregation or their entire day and night activities.

Given the limited research on the annual pelagic movements and pelagic activities of tropicbirds, and devices small enough to be carried by tropicbirds, this family makes a suitable candidate for GLS migratory studies. With specific knowledge gaps in mind, the second half of this thesis will address the following four questions: (1) where are the seasonal core concentrations of a tropicbird species across the non-breeding period? (2) What are the specific routes a non-breeding tropicbird species

uses between core areas? (3) Do male and female tropicbirds exhibit sexual segregation across the non-breeding season? (4) How much time does a specific tropicbird species spend flying compared to resting on the water across the non-breeding period?

Unlike the first half of this thesis, which is strictly hypothesis-based, the majority of the thesis takes an exploratory approach to address the above research questions. My first objective was to identify and map the distribution of Bermuda-origin White-tailed Tropicbirds during the entire non-breeding period. My second objective was to identify the primary core areas birds use during the late-summer period, fall-winter period and spring period, and the routes birds use during these seasons. My third objective was to determine if male and female tropicbirds exhibit pelagic segregation across the entire non-breeding period. Given their solitary feeding style far from breeding sites, we predicted no obvious sexual segregation. My fourth objective was to quantify and describe the at-sea activities of tropicbirds during the non-breeding period. In Bermuda, courting tropicbirds fly among nest sites soon after sunrise, with activity gradually decreasing throughout the late afternoon, until all activity ceases before nightfall. If the non-breeding activities of tropicbirds matches those seen while birds are in Bermuda, I would predict lots of flying activity during the day and little to no activity during night periods.

1.5. Focal species: White-tailed Tropicbird (*Phaethon lepturus catesbyi*)

White-tailed Tropicbird Distribution and Breeding Biology

Given their use of natural and artificial cavities in Bermuda, and the presence of introduced rats and crows on the island, this breeding population of White-tailed Tropicbirds presents a unique opportunity to test the nesting biology hypotheses of this thesis. White-tailed Tropicbirds are the smallest member of the tropicbird family (Phaethontidae), with all three species having predominately white plumage, with varying black on wings and face and unique long, tail streamer feathers (Veit and Jones 2004). Foraging tropicbirds prey on fish and squid, including the Caribbean Reef Squid (*Sepioteuthis sepioidea*; M. A. Mejias unpubl. data), Atlantic Flyingfish (*Cheilopogon melanurus*; M. A. Mejias unpubl.data.) and Needlefish (Belonidae; Le Corre et al. 2003) by plunge diving. White-tailed Tropicbirds are pantropical and breed on remote oceanic islands throughout the southern Indian Ocean, southern and western Pacific and northern and southern Atlantic Ocean. There are six subspecies of White-tailed Tropicbirds: *lepturus* (Indian Ocean), *fulvus* (Christmas Island, Indian Ocean), *dorotheae* (tropical Pacific Ocean), *ascensionis* (Ascension Island, South Atlantic), *europae* (Europa Island, Indian Ocean), and *catesbyi* (Caribbean and Bermuda, Atlantic Ocean) (Le Corre and Jouventin, 1999). Unlike the Bermudian population, which has a finite breeding season in summer, White-tailed Tropicbirds are asynchronous breeders across its tropical range, with breeding occurring all year

(Phillips 1987, Ramos et al. 2005, Malan et al. 2009). Pairs nest inside rocky cavities, crevices and occasionally underneath vegetation (Gross 1912). Females lay single egg clutches and both sexes share an average 42 day incubation. Following hatching, parents rear chicks from 70-91 days (J. L. Madeiros, unpubl. data). epar

Threats facing White-tailed Tropicbirds across their range

White-tailed Tropicbirds are threatened by introduced and native predators across their breeding range. For example, Europa Island, which supports ~ 1000 breeding pairs, has experienced egg and nestling loss by introduced Black Rats (Le Corre and Jouventin, 1999). In addition to Europa Island, rat predation threatens breeding tropicbirds on the four other Îles Éparses, as well as on Puerto Rico, Hawaii and the Bahamas (Harrison 1990, Russel and Corre, 2009). Similarly, introduced feral cats decimated White-tailed Tropicbird colonies on Ascension Island and Fernando de Noronha (J. C. Russell unpubl. data; Ratcliffe et al. 2009). Predation from avian taxa have also been observed. On Europa, tropicbirds lose eggs and nestlings to Pied Crows (*Corvus albus*) and Barn Owls (*Tyto alba*), but whether these predators are native or introduced to the island is unknown (Le Corre and Jouventin, 1997). Introduced mammalian species can also have negative indirect effects on nesting tropicbirds. In Netherlands Antilles, feral goats (*Capra hircus*) trample on tropicbird eggs (Lee and Walsh-McGhee 2000).

Native crabs and skinks are an additional threat to nesting White-tailed Tropicbirds. In Puerto Rico, this species loses many eggs to land crabs (*Gecarcinus)* hermit crabs (*Coenobita clypeatus)* and skinks (*Mabuya sechellensis*) (Schaffner 1991). Tropicbird eggs on Cousin Island, Seychelles face similar threats, particularly by ghost crabs (*Ocypode*; Phillips 1987). Somewhat surprising is the negative effect some native plant species can have on nesting tropicbirds. On Aride Island and Cousin Island, Seychelles, large fruiting events of Grand Devil's Claws (*Pisonia grandis*) produce sticky seeds that adhere to tropicbird feathers, resulting in limited mobility and high mortality in extreme fruiting events (Burger 2005, Catry et al. 2009). Tropicbird nest-cavities are sometimes overgrown with fast growing, dense vegetation, causing breeders to abandon nest sites on Aride Island (Catry et al. 2009). Consequently, loss of nest sites leads to increasing intraspecific competition among White-tailed Tropicbirds, resulting egg loss among the Seychelles and Puerto Rico colonies (Phillips 1987, Malan et al. 2009). Limited nest sites may also explain similar interspecific competition between White-tailed Tropicbirds and the larger Red-billed Tropicbird (*Phaethon aethereus*), the latter species evicting the former from nest-cavities (Lee and Walsh-McGhee 2000).

White-tailed Tropicbird colony in Bermuda: Threats and Conservation

The breeding population of White-tailed Tropicbirds in Bermuda consists of ~ 3,500 breeding pairs and is the largest concentration of this species in the Atlantic Ocean (Lee and Walsh-McGhee 2000, Dobson and Madeiros 2009, J. L. Madeiros unpubl.

data). The breeding season is March-September, when breeders experience similar threats as the global population. For example, the introduced Black Rat is currently the primary mammalian predator of White-tailed Tropicbirds in Bermuda. Although historical accounts mention feral cats and dogs have decimated the Bermudan population, such occurrences have not been reported since the 1980s (Lee and Walsh-McGhee 2000). Introduced American Crows prey on tropicbird eggs and nestlings, with occurrences being observed as early as 1861 (D. B. Wingate pers. comm.).

Bermuda's population of tropicbirds nest predominately in rocky cavities and crevices along the coastline, where breeding sites are threatened by strong weather systems. Hurricane Felix caused severe erosion of Bermuda's southern coastline in the late 1980s, resulting in the loss of 30-50% of rocky cavities (Wingate 1995). Similarly, Hurricane Fabian passed over Bermuda in 2003, demolishing 75% of tropicbird nest-cavities in Castle Harbor, Bermuda (Dobson and Madeiros 2009). Similarly, rising sea level threatens breeders inside low-lying nest cavities (Wingate and Talbot 2003). Introduced trees, including the Australia Pine (*Casuarina spp.*), grow along the rocky coastline and are easily felled during storms, causing their root systems to pull the terrain apart (DW unpubl. data).

These issues have stimulated conservation efforts to aid Bermuda's breeding population of tropicbirds. In the 1960s the Bermuda Department of Conservation Services conducted a mass installation of artificial "igloo" cavities across Bermuda's coastline. The lack of breeding sites in Bermuda was apparent by the rapid occupancy and use of many artificial nests across Bermuda. Despite their occupancy, many

artificial cavities remain unoccupied for unknown reasons. For the artificial cavities that have been occupied, there has yet to be any rigorous scientific experiment examining specific nest-cavity traits possibly affecting nest survival of breeding tropicbirds. Similarly, information on the vulnerability of nest-cavities to predation from introduced rats and crows is not known. As mentioned previously, the first half of this thesis will rigorously test these aspects of this cavity-nesting seabird.

Seasonal residency of Bermudian White-tailed Tropicbirds

Unlike Caribbean breeders, which are present year round and breed asynchronously, the subtropical population of tropicbirds in Bermuda are summer residents with a designated breeding season. Tropicbirds in the Caribbean have a warmer, stable climate year round that likely facilitates year-round breeding, compared to tropicbirds breeding in subtropical Bermuda, where the summers are separated by periods of mild and relatively cool winters, not conducive for breeding. In Bermuda, breeding occurs in March-September, with few post-breeders departing Bermuda as late as November to unknown areas. In 2000, a White-tailed Tropicbird ringing program began, with 1,200 birds being ringed as of 2016 (J. L. Madeiros & M. A. Mejias unpubl. data) where ringed adults and fledglings. Despite this, there have been no reported recaptures of ringed tropicbirds outside of Bermuda. Given the large uncertainty of tropicbird movement, and pelagic activities at-sea, we will use GLS tags to complete the objectives stated above, in order to better understand this important life history stage of this species, while post-breeders are away from breeding colonies.

1.6 Co-authorship statement

Co-authorship statement

This research was co-supervised by Dr. Yolanda Wiersma of Memorial University. I, Miguel Alberto Mejías, hereby declare that I am the primary author of this thesis. As the primary author, I was responsible for majority of the writing of this thesis. This thesis contains two data chapters (i.e., Chapter 2 and Chapter 3). In addition to myself, Chapter 2, entitled Nest-cavity selection and nesting success of Bermudian White-tailed Tropicbirds (*Phaethon lepturus catesbyi*), is co-authored by Dr. David B. Wingate, Mr. Jeremy L. Madeiros, Dr. Yolanda F. Wiersma and Dr. Gregory J. Robertson. Dr. Wingate is the inventor of the artificial cavities for the tropicbirds, and alongside Jeremy Madeiros, installed many of these around Bermuda, making this study possible. Dr. Wiersma helped refine the hypotheses being tested and assisted with the revision of the overall thesis. Lastly, Dr. Robertson helped with analysis of the nest survival data and helped revised the manuscript. Chapter 2 has been submitted and accepted for publication in the *Wilson Journal of Ornithology*. Citation: Mejías, A. M., D. B. Wingate, J. L. Madeiros, Y. F. Wiersma and G. J. Robertson. 2016/7. Nest-cavity selection and nesting success of Bermudian White-tailed Tropicbirds (*Phaethon lepturus catesbyi*). *Wilson Journal of Ornithology*.

Similarly, Chapter 3, entitled Non-breeding distribution and at-sea behaviour of Bermudian White-tailed Tropicbirds (*Phaethon lepturus catesbyi*) in the North Atlantic, is co-authored by Dr. Yolanda Wiersma, Dr. David B. Wingate and Mr. Jeremy L. Madeiros. Dr. Wiersma provided advice with map presentations and,

alongside Dr. Wingate, helped with major revisions, which greatly improving the presentation of this manuscript. Mr. Jeremy Madeiros assisted with the capture and tagging of tropicbirds across Bermuda in 2014. This chapter is in preparation to be submitted for consideration for publication to *The Journal of Field Ornithology*. Potential citation: Mejías, A. M., Y. F. Wiersma, D. B. Wingate, and J. L. Madeiros. 2017. Non-breeding distribution and at-sea behaviour of Bermudian White-tailed Tropicbirds (*Phaethon lepturus catesbyi*) in the North Atlantic. *Journal of Field Ornithology*.

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2. Nest-cavity Selection and Nesting Success of Bermudian White-tailed Tropicbirds (*Phaethon lepturus catesbyi*)

2.1 Abstract

Breeding cavity-nesting seabirds on remote, oceanic islands are threatened largely by destruction of nest cavities and by introduced predators. In response, artificial cavities have been implemented as a conservation strategy. Effective artificial cavity programs require recognition of specific nest-site characteristics, which can be major determinants of survival and persistence of cavity-nesting seabirds. In Bermuda, we monitored 158 natural and 178 artificial cavities of the White-tailed Tropicbird (*Phaethon lepturus catesbyi*) from 2013 to 2015 to determine if specific nest-site characteristics could explain cavity selection, nest survival, and predation by introduced rats (*Rattus* spp.) and American Crows (*Corvus brachyrhynchos*). We found that tropicbirds preferred natural cavities lined with sand, which had smaller entrances and were located on steeper cliffs. Occupancy of artificial cavities on the mainland varied across years and increased with cavity depth, whereas neither variable had any effect on artificial cavity occupancy on satellite islands. Clutch survival declined in cavities with rubble in nesting sand, and those with shallower cavity depths and larger entrance heights. Nestling survival varied by year, declined later in the season and was lower among younger chicks. Rat predation was significantly higher on mainland sites compared to satellite islands. Although crow predation only occurred on offshore island sites, natural cavities and shallower cavities with larger entrance heights were vulnerable. Rat and crow predation rates varied across years. Our results suggest a combination of nest-site characteristics and

temporal factors are important predictors of White-tailed Tropicbird productivity. We recommend conservationists to consider nest-cavity siting, dimensions and practice effective predator control, particularly rats, to improve the nest success of cavity-nesting seabirds.

2.2 Introduction

Nest-site selection has important implications on the survival of terrestrial cavity-nesting seabirds (Ramos et al. 1997, Bourgeois et al. 2014). Ideal breeding locations provide shelter from bad weather, predators, reduce interactions with competitors and offer safety for arrival and departure from cavities (Ricklefs 1969). Factors that can lower reproductive success include flooding of crevices, excessive sun exposure, microclimate, predation, competition for cavities and adults having difficulty accessing nest-sites (Ramos et al. 1997, Thompson and Furness 1991, Kim and Monaghan 2005, Catry et al. 2009, Fontaine et al 2011, Miskelly et al. 2009). Most cavity-nesting seabirds exhibit nest-site fidelity, potentially making them prone to ecological traps if poor conditions persist (Cuthbert 2002, Igual et al. 2007). This pattern may be exacerbated with seabirds nesting on remote oceanic islands, who fail to effectively respond and adapt to alien threats. For example, introduced and feral mammals on islands, such as rats (*Rattus* spp.), cats (*Felis catus*), dogs (*Canis familiaris*) and pigs (*Sus scrofa*) disrupt seabird nest-sites and prey on eggs and nestlings (Challies 1975, Everett 1988, Skira et al. 1996, Ratcliffe et al. 2010, Madeiros et al. 2012, Hervias et al. 2013). Nest cavities on oceanic islands can also be

damaged or destroyed in powerful storms and nest-sites trampled by introduced sheep, goats and cattle (Bell 1955, Wiley and Wunderle 1993, Webster et al. 2005).

Artificial cavities are often provided to reduce predation and mitigate habitat loss in cavity nesting birds (Priddel and Carlile, 1995, Libois et al 2012). Sometimes these measures are effective and enable substantial and rapid population growth (Mazgajski and Rykowska 2008, Corrigan et al. 2011, Madeiros et al. 2012, Sutherland et al. 2014). However, artificial cavities in high densities can attract predators and lead to high nestling mortality; furthermore, poor design (e.g. insufficient insulation) can cause egg or nestling mortality (Dunn 1977, Møller 1989, Klein et al. 2007, Goldingay and Stevens 2009, Björklund, et al. 2013).

Therefore, a successful artificial cavity program requires understanding of whether avian cavity-nesters show preferences for certain characteristics of cavity design and placement, increases nest success and exclude predators. Nest-site selection and success is well studied among terrestrial cavity-nesting birds (Aitken et al. 2002, Goldingay and Stevens 2009, Chalfoun and Schmidt 2012). However, this is not the case for cavity-nesting seabirds on remote islands. Even scarcer in the literature are studies investigating nest-site selection and success of cavity nesting seabirds who also have the option of using artificial cavities. This raises several questions: (1) What are the nest-cavity characteristics of the more frequently used natural and artificial cavities occupied by nesting seabirds? (2) Are some of these nest-cavity characteristics associated with nest success? (3) Are certain nest-cavity characteristics reducing accessibility of cavity contents to introduced predators?

The breeding population of White-tailed Tropicbirds (*Phaethon lepturus catesbyi*) in Bermuda offers an opportunity to address these questions. The species is an obligate cavity nester that uses holes in the limestone cliffs scattered across Bermuda's coastline and satellite islands (Gross 1912, Wingate and Talbot 2003). Bermuda has the largest breeding populations of White-tailed Tropicbirds in the Atlantic (~ 3,500 nesting pairs) and is the most northern breeding population of Phaethon in the world (Wingate and Talbot 2003; Dobson and Madeiros 2009; J. L. Madeiros unpubl. data). Breeding occurs between March and September, with few birds departing as late as November (D. B. Wingate unpubl. data). This population currently faces several threats: coastal erosion of breeding habitat during hurricanes; and predation from the introduced Black Rat (*Rattus rattus*) and Norway Rat (*Rattus norvegicus*) (Gross 1912) and the introduced American Crow (*Corvus brachyrhynchos*), brought to the island by British colonists in the 1860s (D.B. Wingate, pers. comm.). To reduce breeding failure, the Bermuda Department of Conservation Services and some private landowners have installed many artificial cavities, beginning in the 1960s. To our knowledge, this is the earliest artificial cavity program in the world for tropicbirds. We recorded nest-cavity characteristics of natural and artificial White-tailed Tropicbird cavities in order to address the above research questions. We hypothesized that specific nest-cavity characteristics would affect occupancy, nesting success and predation rates of White-tailed Tropicbird cavities (Table 2-1).

2.3 **Methods**

Study area

We studied seven breeding sites on the island of Bermuda (32° 31’ N, 64° 75’ W) and 10 small satellite islands, from April to August, 2013 to 2015 (Fig. 2-1). Nonsuch Island (O on Fig. 2-1) was the largest satellite island site (16 ha) and is the only satellite island with an elevation > 10 meters ASL (Madeiros et al 2012). Out of the 3,500 breeding pairs in Bermuda, ~ 500 - 600 pairs bred among the eastern satellite islands: Southampton Island, Horn Rock, Nonsuch Island and Long Rock (M, N, O and Q, respectively, on Fig. 2-1). About 20 breeding pairs were also monitored on the western offshore sites: Lambda Island, Gamma Island and Rickett’s Island (B, C and D, respectively, on Fig 2-1). Surveys of nesting success have been conducted on many satellite island sites since the 1960s (J. L. Madeiors, unpubl. data).

We monitored mainland sites during the duration of this study. These sites were chosen because they represented coastal breeding habitat: rocky coastal limestone planes, slopes and cliffs riddled with numerous rock cavities. Many inaccessible cavities were located among rocky limestone cliffs ~ 10-15 m high. We suspect these cliff nest cavities to be just as vulnerable to crow predation compared to our surveyed nest-cavities, because crows can fly. However, these un-surveyed cliff cavities would have certainly been less accessible to rats, compared to our surveyed sites. Despite this potential bias, we are confident that our sampled coastal gradient reasonably captures varying tropicbird nesting localities for analysis. Historically, the list of mammalian predators of breeding tropicbirds included the introduced feral dog, feral cat, Brown and Black Rats (DW unpubl. data). Currently, the dominant predators in

Bermuda, and predators of interest in our study, were: the Black Rat (*R. rattus*), an abundant species at all mainland sites throughout the study period, and resident on Nonsuch Island and Long Rock in 2014 and 2015 (Fig. 2-1); and the American Crow, which was present at all study sites across all years.

Nest-cavity searching

In the context of this study we define a nest as the egg deposited by the female, and the cavity as the limestone rocky hole that a tropicbird can lay their egg in. Natural cavities at mainland sites were found by checking any limestone holes and crevices. Additional cavities were found by observing adults arriving at and departing breeding sites. Any natural cavity whose depth and entrance height could accommodate and allowed passage of an adult was considered in the study.

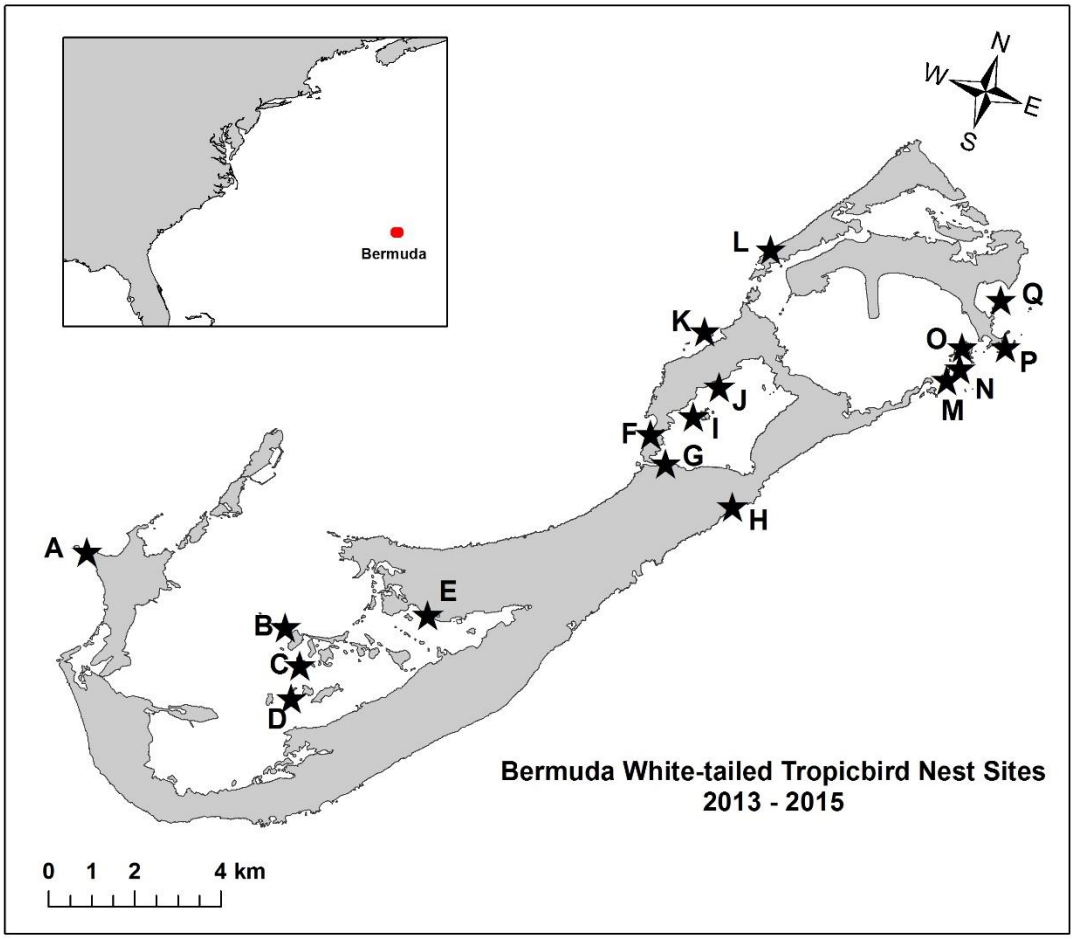

Figure 2-1. Location of White-tailed Tropicbird nest sites across the mainland and satellite islands of Bermuda in 2013-2015. Codes for sites: A, Daniel's Head; B, Lambda Island; C, Gamma Island; D, Rickett's Island; E, Bay House; F, Shelly Bay; G, Bermuda Aquarium; H, Spittal Pond; I, Rabbit Island; J, Cockroach Island; K, Bay Island; L, Ferry Reach; M, Southampton Island; N, Horn Rock; O, Nonsuch Island; P, Cooper's Island; Q, Long Rock.

Unlike the offshore island sites, artificial cavities on the mainland have been largely unmonitored since installation. All artificial cavities were installed in coastal habitat across all sites during 1970-2012. Bermudian artificial cavities were developed as a mass producible fibre bond coated styrofoam hemisphere "igloo" cavity which can be cemented over sandy depressions excavated into level cliff top ledges. This has greatly increased the number of nest sites, making this comparative study possible. For further insulation, additional limestone rocks from the coastline are cemented onto the "igloo" dome, after they are installed. Artificial cavities were 38 cm high and without an entrance tunnel, measure 58 and 62 cm in depth and width respectively and have an entrance height of 12.7 cm. Small, plastic yellow tags, approximately 5 cm long, labelled with a unique identification number were secured to natural and artificial cavities with a stainless steel screw.

Nest-cavity monitoring.

Mainland and satellite island sites were visited every 2-3 weeks in 2013 and 2014 breeding seasons. We initially chose this monitoring schedule in order to limit disturbance to breeders. We tried visiting offshore sites as frequently as mainland sites, but our attempts to land on offshore sites were often hampered by wind direction, which created unsuitable landing conditions. We found that White-tailed Tropicbirds grew accustomed to our nest checks, so we increased our sampling to weekly for mainland sites in 2015, and resumed our regular schedule for offshore sites. During each visit all cavities were checked and contents recorded. We considered a cavity occupied if an egg, chick or remains of either was present inside a nest-cavity.

Accessible adults sitting inside cavities were carefully lifted with a 75 cm flat, wooden stick to confirm the presence of an egg or chick. The cavity contents of adults who were not within reach had to be confirmed either when the adult was absent or after hatching. When adults in such nest-cavities were absent, usually soon after nest failure, we could readily detect if breeding failure occurred by the presence of a flattened egg, bits of eggshell or remains of a nestling on the nest cavity floor. The breeding activity of some nest cavities remained unknown due to lack of evidence of bird visits or complex layout of the cavity; thus we excluded these nest cavities from our analysis. A nest was considered successful either if a chick fledged or if a chick ≥ 7 weeks old remained inside a cavity by the end of the study period. We chose this age criteria because previous studies found chick mortality to be higher among younger chicks (Phillips 1987; Malan et al. 2010).

Nest-cavity characteristics.

Eight physical nest-site attributes believed to determine occupancy, breeding success and predation were recorded (Table 2-1). However, attributes of all cavities were not available. We considered a cavity to contain nesting sand if it had enough sand to cover the entire floor where birds sat. A cavity was considered to have rubble if rubble or rocks were present in the sand. We measured cavity depth and entrance height with a metallic and plastic tape measure respectively (± 1 cm). To reduce disturbance to cavity inhabitants, we took cavity dimensions either before a cavity became active or after fledging. To calculate slope of coastal terrain, we obtained a geographic information system (GIS) geodatabase containing a digital elevation model of

Bermuda from the Bermuda Department of Environment and Natural Resources. This geodatabase also had a shapefile containing points representing all nest-cavities under observation. We used the intersect analysis tool in ESRI ArcMap 10 GIS to assign a coastal slope value to all tropicbird cavities. To calculate the number of neighboring nest cavities per nest cavity, we created 3 m buffers around each tropicbird nest in ArcMap, similar to Bourgeois and Vidal (2007). In Bermuda, tropicbirds nested in relatively high densities, with most nest cavities having at least one neighbor within 3 m of a single natural or artificial nest cavity (pers. obs.).

The two primary predators of interests in our study were Black Rats and American Crows. We distinguished rat and crow predation by closely inspecting eggs to distinguish them from broken eggs (Fig. 2-2). Eggs were considered broken if they contained cracks and punctures without any tooth or peck holes from predators. Eggs that contained chew marks or neat peck holes were considered to be predated by rats and crows respectively. In cases where the entire egg or chick was missing, predator identification was recognized by rat or crow prints in the nesting sand. Due to the recolonization of rats on Nonsuch Island and Long Rock in 2014, the identification of the predator of stolen eggs and chick where rats and crows overlapped and prints were not found was not possible.

Table 2-1. Variables recorded from White-tailed Tropicbird nest-cavities expected to influence cavity occupancy, nest success and predation between 2013– 2015. Expected increase (↑) and decrease (↓) of response variables for the appropriate independent variables are shown. Cavity selection variables only applied to natural cavities are denoted with (*). Independent variables that were not tested towards a specific dependent variable are denoted with (X).

Variables	Description	Cavity selection	Clutch survival	Chick survival	Predation
Cavity type	Natural (0), Artificial (1)	X	↑ in (1)	↑ in (1)	↓ with (1)
Cavity location	Mainland (0), Offshore Is. (1)	↑ in (1)	↑ in (1)	↑ in (1)	↓ with (1)
Nesting sand*	Absent (0), Present (1)	↑ in (1)	X	X	X
Rubble in sand*	Absent (0), Present (1)	X	↓ in (1)	X	X
Cavity depth	Maximum length from the entrance to back of cavity (cm)	↑ with depth	↑ with depth	↑ with depth	↓ with depth
Entrance height*	Maximum height of cavity opening from the lip to the ground (cm)	↓ with height	↓ with height	↓ with height	↑ with height
Coastal slope*	Maximum slope of coastal terrain where nest cavity resides (°)	↑ with slope	↑ with slope	↑ with slope	↓ with slope (rats)
Neighbor numbers	Number of nest-cavities occupied by other breeders within 3-m radius around active focal nest-cavity	X	↓ with neighbors	↓ with neighbors	↑ with neighbors

Figure 2-2. Photos of failed White-tailed Tropicbird eggs depicting 3 distinct forms of damage: (A) broken egg, (B) rat predation and (C) crow predation. Broken eggs were often cracked in half, sometimes completely flattened, and lacked the characteristic chew marks of rats or peck holes from tropicbird hatchlings. The remains of rat predated eggs were characterized by teeth marks running along the circumference of the egg. Crow predated eggs exhibited a large, single, triangular peck hole on either side of the egg. Photos by MM.

Statistical analyses

Nest-cavity Characteristics

We used two-tailed independent t tests (with $\alpha = 0.05$ in these and other statistical tests described below) to compare occupied natural and occupied artificial cavities on the variables cavity depth, entrance height, coastal slope and number of neighbors. Results of t tests are presented with respective t scores, degrees of freedom and *P* values.

Nest-site selection

We used generalized linear models (GLMs: logit link function, binomial distribution) to test for a relationship of specific nest-site characteristics on the occupancy of natural and artificial cavities (Table 2-1). More specifically, we used GLMs to test whether available natural nest-cavities were used based on cavity location, presence of nesting sand, year, cavity depth, entrance height and slope of coastal terrain. Similarly, we applied GLMs to determine if available artificial cavities were used based on cavity location, year and cavity depth. All artificial cavities were installed with nesting sand, similar entrance heights and along steep coastal cliffs. We assumed rubble in nesting sand only had survival implications for clutches and not affect cavity occupancy, nestling survival or predation rates, and was therefore excluded from the latter three models. Lastly, neighbor numbers was only measured for occupied cavities and therefore could not be used to explain nest-site selection in our study. Results of GLMs are presented with respective Wald's statistic, degrees of freedom and *P* values.

Clutch and nestling survival

For each year of the study we report the percentage of eggs laid that hatched (i.e., hatching success), the percentage of hatchlings that fledged (i.e., fledging success) and the percentage of eggs that produced fledglings (i.e., breeding success) for all 3 seasons. Due to infrequent sampling of offshore sites, the approximate laying date for unsuccessful clutches was not possible because tropicbirds have single egg clutches, thereby preventing estimates of nest age by observing additional eggs being laid by the female, as seen with songbirds (Nur et al. 2004). We estimated clutch and nestling survival using the nest survival model in Program MARK (White and Burnham 1999; Dinsmore et al. 2002; Rotella et al. 2004). This model estimates the probability a nest survives a single day within a given breeding season, defined as daily survival rate. Unlike Mayfield's basic nest survival model, Program MARK does not require precise dates on hatching or failure (Mayfield 1961, 1975). The Program MARK model is an advanced extension of the Mayfield estimate, removing search effort effects from an observer's ability to locate nests, which are of various ages and allowing variables of interest to be added (White and Burnham 1999).

We used eight variables, without interactions, to test whether they affected clutch survival: cavity type, cavity location, rubble in nesting sand, year, cavity depth and entrance height, coastal slope and neighbor numbers. (Table 2-1). Due to uncertainty in specific egg laying dates for some eggs, we did not apply any continuous temporal factors in our clutch survival models. Nine variables, without interactions, were analyzed to test whether they affected nestling survival: cavity type, cavity location,

year, cavity depth, entrance height, coastal slope, neighbor numbers, day of the year and nestling age (Table 2-1). We used a model selection approach using Akaike's Information Criterion (AIC; Burnham and Anderson 2002). Models were ranked based on their ΔAIC value was used for inference (ΔAIC_c), with models $\Delta AIC_c \leq 4$ considered plausible (Burnham and Anderson 2002), corrected for small sample size. Model building began with the construction of the null model (intercept only), followed by individual nest-site variable models, in order to examine main effects on clutch and nestling survival (Dinmore et al. 2002). Lastly, we built models with varying combinations of independent variables hypothesized to be important determinants of clutch and nestling survival. A logit link function was applied to all models.

Black Rat and American Crow predation

We used generalized linear models (GLMs: logit link function, binomial distribution) to test the relationship of Black Rat and American Crow predation to specific nest-site characteristics (Table 2-1). Seven variables were used for rat predation: cavity type, cavity location, year, cavity depth, entrance height, coastal slope and neighbor numbers; five variables for crow predation GLMs: cavity type, year, cavity depth, entrance height and neighbor numbers. Although coastal slope was used in our rat predation model, it was excluded from our crow predation GLM because we assumed coastal slope would not hinder foraging crows due to flight. Similarly, all crow predation events were recorded on offshore islands, thus we did not include cavity location in our crow predation model. Results are presented with respective

Wald's statistic, degrees of freedom and *P* values. All t tests and generalized linear models were run in R (version 2.12.) (R Development Core Team 2010).

2.4. Results

Nest-cavity characteristics

We monitored 158 natural and 178 artificial White-tailed Tropicbird cavities. Natural and artificial cavities differed in two characteristics: natural cavities were deeper and had higher entrances than artificial cavities (Table 2-2).

Nest-cavity selection.

We found no relationship between natural cavity occupancy and cavity location (W = -0.74, df = 375, *P* = 0.46).

Table 2-2. Descriptive statistics of natural and artificial cavities used by White-tailed Tropicbirds breeding in Bermuda, 2013– 2015. The mean ± SD for cavity types are shown outside parentheses and values inside parentheses show range and sample size.

	Type of nest:	
Variable	Artificial	Natural
Cavity depth (cm) [a]	82.0 ± 29 (32 – 203; 132)	103 ± 54 (30 – 365; 116)
Entrance height (cm) [b]	16.6 ± 4.52 (7.62 – 34.30; 132)	25.0 ± 13 (8 – 84; 116)
Coastal slope (degrees) [c]	29.5 ± 13 (0 – 53; 115)	27.5 ± 11.0 (5.78 – 55.70; 96)
No. neighbors[d]	1.00 ± 1.00 (0 – 4; 129)	1.00 ± 1.04 (0 – 5; 104)

[a] $P < 0.001$ ($t_{172} = 3.91$)

[b] $P < 0.001$ ($t_{141} = 6.84$)

[c] $P = 0.23$ ($t_{209} = -1.20$)

[d] $P = 0.18$ ($t_{211} = -1.32$)

Due to a significant interaction between cavity location and cavity depth in our artificial nest-site selection model, we considered only cavity depth and year as explanatory variables for the occupancy of artificial cavities, because the occupancy of shallow and deep artificial cavities significantly differed between locations (W = 5.84, df = 519, $P < 0.001$).

Natural cavities with nesting sand had higher occupancy than those without (W = 4.55, df = 375, $P < 0.001$). We found no relationship between occupancy of natural cavities and year (Wald statistic: W = 1.14, df = 375, $P = 0.26$). Occupancy of mainland artificial cavities increased with year (W = 2.44, df = 285, $P = 0.01$), whereas occupancy of offshore artificial cavities did not vary with year (W = 1.79, df = 235, $P = 0.23$). There was no relationship between natural cavity occupancy and cavity depth (W = 0.04, df = 375, $P = 0.97$). Occupancy of artificial cavities on the mainland increased with cavity depth (W = 7.04, df = 285, $P < 0.001$), whereas offshore artificial cavity occupancy was not affected by cavity depth (W = -1.81, df = 235, $P = 0.06$). Tropicbirds occupied natural cavities with smaller entrance heights compared to natural cavities with larger entrances (W = -2.45, df = 375, $P = 0.01$). Natural cavities on steeper coastal slopes had higher occupancy than those on flatter terrain (W = 2.72, df = 375, $P = 0.007$).

Clutch survival

We observed 566 clutches in the study (Table 2-3). In total, 43% (n = 245) of clutches were inside natural cavities and 57% (n = 321) of clutches were inside artificial cavities. Our nest monitoring season, from the first to the last date of cavity monitoring, was 151 days in all years. Birds exhibited high nest cavity fidelity, a clutch size of one, and were likely to re-nest if their first attempt failed. In total, 93% (n = 529) of clutches were first attempts and the remaining 7% (n = 37) were replacement clutches. Clutch replacement was very common among Bermudian White-tailed Tropicbirds pairs throughout most of the breeding season. Across all three years, re-nesting occurred in May (n = 7), June (n = 20) and July (n = 9). The primary cause of total clutch failure (in order of frequency) were egg breakage and predation from crows and rats (Table 2-4).

Rubble in nesting sand, cavity depth and entrance height were important determinants of White-tailed Tropicbird clutch survival (Table 2-5). Across all models, rubble, cavity depth and entrance height had summed parameter weights of 0.96, 0.99 and 0.97 respectively. The top model indicated that clutch survival declined with rubble within nesting sand (β_R = -0.54, SE = 0.18, 95% CI = -0.90, -0.18), increased with increasing cavity depth (β_{CD} = 0.01, SE = 0.003,

Table 2-3. The total number of clutches, nestlings and nest success of White-tailed Tropicbird nests in Bermuda in 2013 – 2015. Numbers inside and outside brackets correspond to natural and artificial cavities respectively.

Year	No. clutches	No. nestlings	Hatching success (%)	Fledging success (%)	Breeding success (%)
2013	91 (94)	25 (37)	27 % (39%)	96% (100%)	26% (39%)
2014	66 (105)	40 (66)	61% (63%)	88% (83%)	53% (52%)
2015	88 (122)	52 (76)	59% (62%)	63% (89%)	38% (56%)
Total	566	296			

Table 2-4. Causes of nesting failures among eggs and nestlings of breeding White-tailed Tropicbirds in Bermuda in 2013 – 2015. Codes for letters: C, American Crows; R, Black Rats; A, Argentine Ants; U, unknown predators (rat or crow)**.**

	Causes of egg mortality:				Causes of chick mortality:		
Year	Break.	Pred.	Aband.	Unk.	Hatch.	Pred.	Unk.
2013	4	1R, 19C	0	10	0	1R	0
2014	22	1R, 5C, 2U	3	0	0	3R, 1A, 6U	5
2015	35	12R, 4C, 6U	3	1	3	8R, 1C, 4A, 3U	8
Totals	60	13R, 28C, 8U	6	11	3	12R, 1C, 5A, 9U	13

95% CI: 0.006, 0.01), and declined with increasing entrance height (β_{EH} = - 0.03, SE = 0.008, 95% CI = -0.04, - 0.01). To estimate the effect of cavity depth and entrance height on clutch survival individually, we ran 2 models looking at both independently. The probability of a clutch surviving the mean incubation period (i.e., 42 days) inside the shallowest cavities was 0.58, compared to 0.99 within the deepest cavities (β_{CD} 95% CI = 0.004, 0.01; Fig. 2-3A). The probability of clutch surviving the mean incubation period inside cavities with the smallest entrances was 0.81 compared to 0.29 clutch survival inside cavities with the largest entrances (β_{EH} 95% CI = -0.03, -0.006; Fig. 2-3B). Relationships among cavity type, location and year were weak (95% CI overlapped 0 for all of these variables).

Table 2-5. Model selection results for testing hypotheses about the effects of nest-site characteristics and breeding season on Bermudian White-tailed Tropicbird clutch survival. Models with weights (w) < 0.01 not shown below.

[a] Number of parameter estimates

[b] Model likelihood

[c] Akaike's information criterion

[d] Difference in AICc values of the current and top-ranked model's AICc

[e] Weight of evidence supporting models

[f] Deviance not explained by each model

Model	K[a]	Model Likelihood[b]	AICc[c]	ΔAICc[d]	w[e]	Deviance[f]
Rubble + Cavity depth + EH	4	1.00	855.6	0.00	0.93	847.6
Global Model	10	0.02	863.2	7.62	0.02	843.2
Cavity type + Rubble + Cavity depth	4	0.02	863.9	8.26	0.01	855.9
Cavity type + Cavity depth + EH	4	0.01	864.2	8.63	0.01	856.2
Location + Cavity depth + EH	4	0.01	864.4	8.78	0.01	856.4

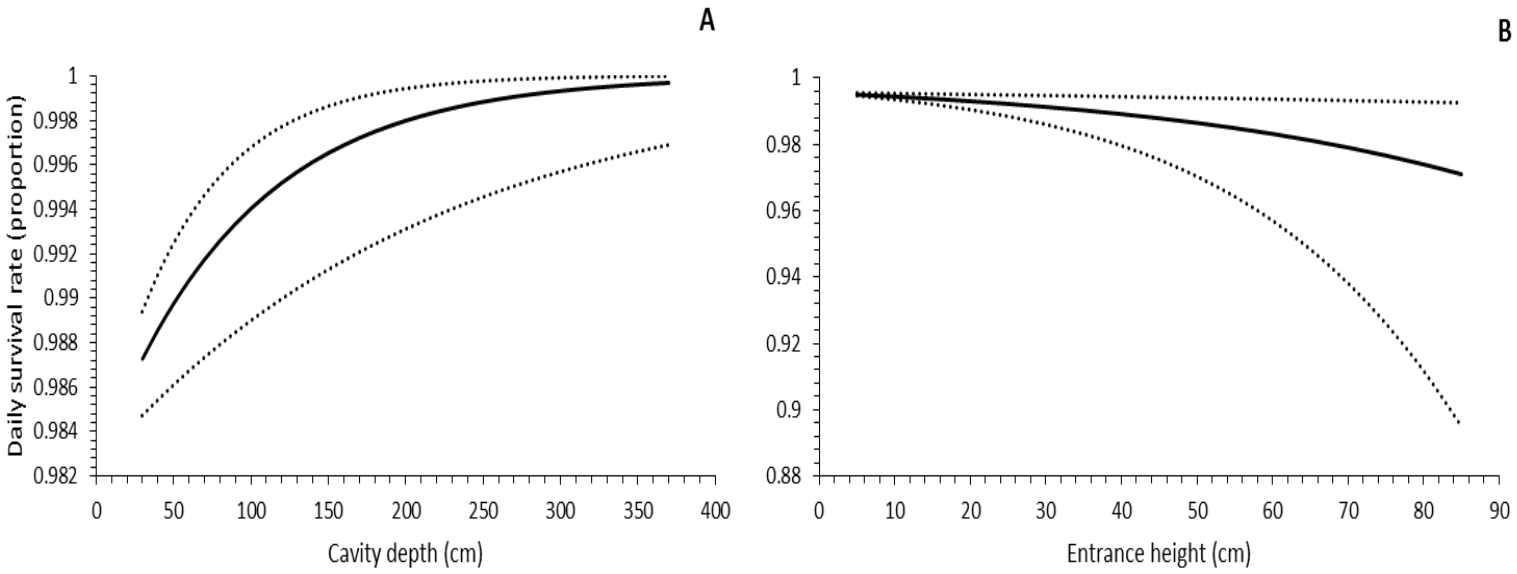

Figure 2-3. Daily survival rates estimated with Program MARK and 95% confidence intervals of Bermudian White-tailed Tropicbird clutches across nest-cavities of varying cavity depths (A) and varying entrance heights (B) from 2013 – 2015. The results of the clutch survival and entrance height model contained only the cavity depth and entrance height covariate. Clutch survival was predicted using the mean incubation period (42 days) of White-tailed Tropicbirds. Clutch survival was lower in shallower cavities and steadily increased as cavities deepened. Clutch survival was higher in cavities with smaller entrances and slightly decreased as entrance heights increased.

Nestling survival.

We monitored 296 nestlings across the 3 year study period (Table 2-3). Nestlings were followed 70 – 91 days after hatching or until death occurred. Main contributors of nestling mortality included rat, crow and Argentine Ant (*Linepithema humile)* predation (Table 2-4). Nest survival models (from Program MARK) indicated year, day of year and nestling age were important predictors of White-tailed Tropicbird nestling survival (Table 2-6).

Across all models, 2014, 2015, day of year and nestling age had summed AICc weights of 0.98, 0.99, 0.96 and 0.99 respectively (Table 2-6). In the top model, nestling survival was lower in 2014 (β2014 = -2.41, SE = 1.03, CI = -4.44, -0.38), and 2015 (β2015 = -2.93, SE = 1.02, CI = -4.93, -0.93) compared to 2013, declined as the season progressed (βDayOfYear = -0.02, SE = 0.008, 95% CI = -0.04, -0.009) and increased with nestling age (βAge = 0.15, SE = 0.02, 95% CI = 0.11, 0.19). To examine the effect size of nestling age on nestling survival, we ran a model consisting only of this variable. This model indicated nestling mortality to be highest during the first twenty days of life, with survival remaining very high during later days (95% CI = 0.08, 0.16; Fig. 2-4). Cavity type, location, cavity depth and entrance height all exhibited weak effects on nestling survival (95% CI overlapped 0 for all of these variables).

Table 2-6. Model selection results for testing hypotheses about the effects of nest-site characteristics and breeding season on Bermudian White-tailed Tropicbird nestling survival. Models with weights (w) < 0.01 not shown below.

[a] Number of parameter estimates

[b] Model Likelihood

[c] Akaike's information criterion

[d] Difference in AICc values of the current and top-ranked model's AICc

[e] Weight of evidence supporting models.

[f] Deviance not explained by each model.

Model	K[a]	Model Likelihood[b]	AICc[c]	ΔAICc[d]	w[e]	Deviance[f]
2014 + 2015 + Time + Age	5	1.00	305.1	0.00	0.94	295.1
2014 + 2015 + Age	4	0.03	311.9	6.87	0.03	304.0
2015 + Time + Age	4	0.01	313.7	8.64	0.01	305.7
Global model	11	0.01	314.0	8.92	0.01	292.0

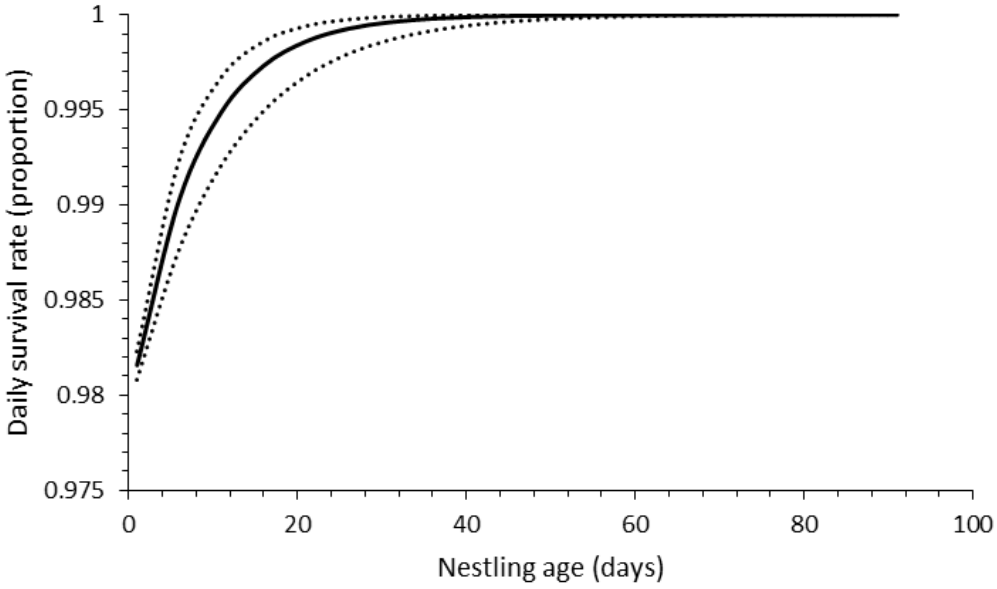

Figure 2-4. Daily survival rates estimated from Program MARK and 95% confidence intervals of Bermudian White-tailed Tropicbird nestlings across a 91 day period from 2013-2015. These results are from the nestling survival model containing only the nestling age covariate. Nestling survival was predicted using the mean fledging period (77 days) of White-tailed Tropicbirds. Nestling survival is lower among younger chicks but increases and remains constant after 20 days old.

Black Rat and American Crow predation.

Rat and crow predation events are summarized in Table 2-4. Rat predation did not differ between natural and artificial cavities (W = -0.11, df = 467, $P = 0.91$). Crow predation was higher amongst natural cavities compared to artificial cavities (W = 3.49, df = 252, $P < 0.001$). Rat predation was higher on mainland sites, compared to satellite islands (W = 2.68, df = 467, $P = 0.007$). Rat (W = 3.69, df = 467, $P < 0.001$), and crow predation (W = -3.55, df = 252, $P < 0.001$) varied across years. We found no relationship of rat predation and cavity depth (W = 0.59, df = 467, $P = 0.56$). Crow predation was higher amongst shallower cavities compared to deeper cavities (W = -3.56, df = 252, $P < 0.001$). Rat predation was not affected by entrance height (W = 1.30, df = 467, $P = 0.19$), whereas crow predation was higher among cavities with larger entrance heights (W = 2.16, df = 252, $P = 0.03$). Rat predation was not affected by steepness of coastal slope (W = 0.32, df = 469, $P = 0.75$). We found no relationship between rat (W = -0.45, df = 467, $P = 0.65$) and crow (W = 1.88, df = 257, $P = 0.06$) predation and neighbor numbers.

2.5 Discussion

We found that nest-cavity occupancy, egg and chick mortality of White-tailed Tropicbirds in Bermuda were related to nest-site characteristics and temporal factors. Furthermore, these relationships differed between natural and artificial nest cavities. Tropicbirds preferred natural nest cavities with nesting sand, smaller entrance heights

and located on steeper cliffs. The sandy substrate protect eggs from the hard, jagged limestone floor, which could puncture eggs during incubation. Smaller entrances may reduce accessibility and detectability from predators, as seen with the Magellanic Penguin (*Spheniscus magellanicus*, Stokes and Boersma 1998) and the Whiskered Auklet (*Aethia pygmaea*, Hunter et al. 2002). In a study of breeding White-tailed Tropicbirds in the Seychelles, Phillips (1987) suggested nest-cavities with larger entrances leave nest inhabitants prone to chronic sun exposure, causing heat stress of adults and high nestling mortality.

We predicted that natural nest cavities on steeper cliffs would be preferred because they would be less assessable to mammalian predators, such as rats (Oro et al. 2004, Igual et al 2006). However, rats were able to reach nests, regardless of coastal slope; likely a consequence of their small size. Historically, dogs were a major predator of tropicbird nests on flatter terrain and large entrance accessible nest-cavities up until the 1980s, when more effective control of feral dogs took effect (DW unpubl. data). While dog predation was not recorded in this study, it is obvious that vertical cliff holes are less accessible to them. Alternatively, natural cavities on steeper cliffs may be favorable because they allow easier arrival and departure for tropicbirds, because tropicbirds move poorly on the ground on account of their short tarsi (Clark et al. 1983).

We found no evidence that tropicbirds favored deeper natural nest cavities, however, they had higher breeding success in them. Our results differed from previous studies, where deeper natural cavities were used by cavity-nesting seabirds, including

shearwaters and petrels (order: Procellariiformes, Schramm 1986, Bourgeois and Vidal 2007, Buxton et al. 2015). In Bermuda, natural nest cavities are lost through hurricanes. In 2003, Hurricane Fabian destroyed ~ 75% of nest-cavities among eastern sites (Wingate and Talbot 2003, Dobson and Madeiros 2009). Therefore, the Bermudian population of White-tailed Tropicbirds may be constrained by the availability of natural nest cavities remaining. Thus, shallower natural nest cavities suffice in the absence of predators, as long as they provides sufficient shade and shelter from rain, as seen with nesting White-tailed Tropicbirds in nest cavities partially concealed from above in Aldabra (Prys-Jones and Peet 1980), Round Island (Burger and Gochfeld 1991), Seychelles (Hart et al. 2016) and underneath large boulders on Cousin Island, Seychelles (Phillips, 1987).

For artificial nest cavity selection, occupancy of shallower and deeper artificial cavities varied with location. Tropicbirds occupied deeper artificial cavities on mainland sites, whereas cavity depth did not affect occupancy on artificial nest cavities on offshore islands. The relative absence of mammalian predators and inhabitants on offshore sites allow tropicbirds to readily occupy shallower artificial cavities. Additionally we found tropicbirds nesting underneath vegetation on many offshore sites, a behaviour seldom seen on the mainland, emphasizing a difference in nest-site use between mainland and offshore nesters (pers. obs.). We also found a significant increase in occupancy of mainland artificial nest cavities, from 32%, to 45% to 47% in 2013, 2014 and 2015 respectively. A similar trend was seen with European Storm-Petrels (*Hydrobates pelagicus*) nesting in artificial boxes (de León

and Mínguez 2003). The gradual increase of artificial nest cavity occupancy on the mainland may also reflect the restoration of micro-colonies in areas previously affected by coastal development, whereas the consistently high occupancy of offshore artificial nest cavities reflects the complete saturation of offshore nest sites from the high concentration of breeding birds among undeveloped habitat.

As predicted, rubble in nesting sand had a strong negative effect on clutch survival. Stones intermingled with nesting sand can puncture an egg during incubation, like the Madeiran Storm-Petrel (*Oceanodroma castro*; Bolton et al. 2004). We also observed severe fights within the vicinity of nest cavities, which might have resulted in clutch loss, similar to tropicbirds in Puerto Rico (Schaffner 1991). Crow predation caused clutch failure in shallower nest-cavities, with larger entrances. Higher nest success in deeper natural cavities also seen with the Yelkouan Shearwater (*Puffinus yelkouan*, Bourgeois and Vidal 2007, Bourgeois et al. 2014) and Cory's Shearwater (*Calonectris borealis*, Ramos et al. 1997).

Nestling survival of Bermudian White-tailed Tropicbirds was strongly influenced by temporal factors of year, time of nesting period and nestling age, rather than physical characteristics of nest-cavities. Annual variation in nest success is a well-documented phenomenon among breeding seabirds (Croxall and Rothery 1991, Chastel et al. 1993). We found nestling survival was lower in 2014 and 2015 compared with 2013. In 2013, we only recorded one chick death, caused by a rat. Whereas 2014 and 2015 marked the increase in rat predation of nestlings. It should be noted our 2013 data may have underestimated actual nestling mortality because our

sampling that year ended with many young nestlings still being reared and whose fates were unknown. We discovered the remains of several young nestlings being devoured by Argentine Ants towards the end of the nesting period. Nestlings belonging to late breeders are being reared during the hottest and driest parts of the summer, conditions that facilitate increasing foraging effort and range expansion of Argentine Ants (Sanders et al. 2001, Heller and Gordon 2006). However, the Argentine Ant is currently restricted to the mainland of Bermuda, sparing offshore island nesters. These observations suggest that tropicbirds would have higher breeding success if they nested earlier in the season (i.e., April), as opposed to beginning nesting from June onwards.

The most important predictor of Bermudian White-tailed Tropicbird nestling survival was nestling age. Younger chicks suffered higher mortality than older chicks. Our findings are similar to White-tailed Tropicbirds breeding on Aride Island and Cousine Islands of Seychelles (Ramos et al 2005, Malan et al. 2009). Nestlings 1-3 weeks old were most vulnerable to rat, crow and ant predation, echoing the trend of younger petrel chicks being predated by house mice (*Mus musculus L.*) on Gough Island (Dilley at al. 2015). Nestlings this age are too small to defend themselves and have downy feathers that are not as impervious to ant predation as the contour feathers of older nestlings. Unlike clutch survival, none of our nest-site characteristics affected nestling survival. This can best be explained by differences in cavity accessibility of the predators of eggs and nestlings. Clutch predation was due largely to crows that

were limited by physical dimensions of nest-cavities. Whereas nestlings were predated largely by smaller rats, which accessed nestlings, regardless of nest cavity dimensions.

We found rat predation to be similar between nest cavity types, whereas natural cavities were more prone to crow predation, compared with artificial nest cavities. Natural nest cavities had larger entrances than artificial cavities, making them more readily visible and vulnerable to crows. Higher rat predation on mainland sites was not surprising for two reasons. First, offshore sites are not as readily accessible to the rat population of the mainland, which are known to be abundant across the island of Bermuda (J. L. Madeiros and D. B. Wingate unpubl. data). Second, rat control efforts are used on many offshore sites, keeping some rat free and others with reduced numbers (J. L. Madeiros and D. B. Wingate unpubl. data).We also observed a strong positive and negative relationship of year with rat and crow predation respectively. The diet of rats often shows high plasticity on seabird islands and their numbers can show annual fluctuations depending on specific island conditions (Martin et al. 2000, Major et al. 2007). We interpret annual differences in rat predation as changes in the abundance of alternative prey items. Crow predation, however, showed a strong decline across the study period. Crow predation was caused by a small, specialized flock of 8-10 birds, whose numbers were reduced to ~ 5 birds through selective culling. A similar culling effort of 16 specialized predatory Yellow-legged Gulls (*Larus michahellis*) increased nesting success of European Storm-Petrels over 3 years (Sanz-Aguilar et al. 2009).

Contrary to our prediction, neighbor numbers did not affect crow predation. High nest densities can facilitate increased predation of nest-cavities by crows (Sugden et al. 1986) and weasels (*Mustela nivalis*, Dunn 1977). However, our study undoubtedly underestimated the number of crow predation events, and the use of camera traps could have remedied this limitation (Hervias et al. 2013). Nonetheless, all crow predation was confined to the Castle Harbor Islands, which supports the largest concentration of breeding tropicbirds in Bermuda, possibly indicating density dependence, but at a larger scale.

Although crow predation can be controlled by simple modifications of nest cavity dimensions, smaller predators like rats and Argentine Ants, the latter pest presently absent from all offshore islands, pose a higher threat to nesting tropicbirds. Unlike rats, which can be removed with intensive baiting and live trapping, removal of Argentine Ants would be nearly impossible because their colony size can rapidly increase by the thousands (Hee et al. 2000). Likely avenues of ant invasion would be day visitors and researchers from ant-infested areas on the mainland, travelling to offshore islands via boat. Such transportation is already known to increase the chance of inadvertent introduction of invasive species (Reaser et al. 2007, Oppel et al. 2011). With these threats in mind, several biosecurity measures are currently being practiced, particularly on Nonsuch Island: (1) checking shoe soles and baggage for unwanted insects and seeds and (2) scrubbing shoes soles in provided quarantine footbaths at the landing dock. Although these measures have proven to be effective in keeping ants off, signage on the less restricted offshore islands that inform visitors of such risks

would undoubtedly be beneficial, and in the long term preserve the nesting habitat of our native seabirds.

Conservation Implications. — Our findings highlight the consequences certain nest-site characteristics have on cavity-nesting seabirds, and could be of importance to managers. First, even if artificial cavities produce fledglings at similar rates as natural cavities, installing them would still benefit the targeted population by providing additional nesting space. Second, location of artificial cavity installment should carefully be considered because differences in habitat quality may result in low occupancy or seabirds favoring a nest-site trait in one location but not in the other. Third, improving nest success, specifically with clutches, can be accomplished by ensuring nesting sand is free of small stones. Fourth, if the cavity nesting bird of interest shows no strong preference in cavity dimensions, like cavity depth, we recommend fitting cavities with deeper tunnels, as well as smaller entrances, to reduce predation risk from avian predators. This would be especially beneficial if avian predators cannot be removed from colonies. Lastly, smaller predators, like rats and ants, are likely to enter cavities regardless of cavity dimensions. Therefore, biosecurity measures should be taken in order to prevent these predators from reaching breeding colonies. If invasions of these pests do occur, immediate baiting and live capture measures should be taken before their numbers increase, thus ensuring the persistence of breeding cavity nesting seabirds.

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3. Non-breeding Distribution and at-sea Behaviour of Bermudian White-Tailed Tropicbirds *Phaethon lepturus catesbyi* in the North Atlantic

3.1 Abstract

Advances in technology have given researchers the ability to track and quantify behaviour of migratory seabirds outside of their breeding season. Using small light-based geolocators, we identified the non-breeding distribution and pelagic activity of 25 adult White-tailed Tropicbirds (*Phaethon lepturus catesbyi*) from Bermuda between July 2014 and May 2015. Our study found that after breeding, 72% of birds spent most of the late summer (July - September) in Bermudian waters; by early September most birds took a direct easterly route from the island. During the fall and winter (October-February) birds inhabited waters from Bermuda to as far east as the Mid-Atlantic Ridge. By spring (April-May) all individuals were in waters between Bermuda and the British Virgin Islands. All birds then followed a general northern route, with variations in timing, returning to breeding sites in April-May. Behaviorally, male and female birds had similar at-sea behavior patterns. In total, tropicbirds spent 95% of night periods and 59% of day periods on the water during the non-breeding season. To our knowledge, these findings provide the first information on the non-breeding distribution and at-sea behavior of an Atlantic tropicbird species. Our study identifies areas where White-tailed Tropicbirds may be vulnerable outside the breeding season and where conservation efforts to minimize at-sea threats should be taken.

3.2 Introduction

Pelagic seabirds represent a diverse group of species whose terrestrial breeding biology is well known, but whose distribution and activities outside the breeding season are poorly known. Data on their pelagic range traditionally came from ship surveys and ringed recoveries (Briggs and Chu 1986, Clarke et al. 2003, Gaston et al. 2008, Olmos 2013). Advances in technology now grant researchers tools to fit breeding seabirds with small, tracking devices to get more detailed data on movement than previously available. For example, small (1g) and inexpensive archival light-based geolocators (GLS loggers) can record locational and salt water immersion data for years (Afanasyev 2004). Although GLS loggers have inherent weaknesses, notably high errors in estimates of spatial coordinates, they are adequate for identifying core pelagic areas of non-breeding seabirds at a global scale (Phillips et al. 2004a).

The small size of GLS loggers make them ideal for identifying the non-breeding distributions and ecologically important areas of smaller avian species, like the Arctic Tern (*Sterna paradisaea*; Egevang et al. 2010), Leach's Storm-Petrel (*Oceanodroma leucorhoa*; Pollet et al. 2014) and Semipalmated Sandpiper (*Calidris pusilla*; Weiser et al. 2016). These devices can also identify potential overlaps with longline fishing and pollution, as seen with the Flesh-footed Shearwater (*Ardenna carneipes*; Thalmann et al. 2009) and Laysan Albatross (*Phoebastria immutabilis*; Young et al. 2009) respectively. Additionally, knowing the sex of tagged birds permit studies on pelagic segregation between males and females; a consequence of size-mediated competitive exclusion, or niche or prey specialization (Nel et al. 2002, Phillips et al.

2005, 2007, 2011). The flight and resting periods of seabirds can also be estimated from the salt water immersion data from GLS loggers. Immersion data show that some non-breeding seabirds are active during the day, while others more so at night (Hedd et al. 2012, Dias et al. 2015). These temporal differences reflect distinct foraging strategies, where some seabirds rely on fish driven to the surface by foraging tuna during the day versus those that feed on prey that come to the surface at night (Yamamoto et al. 2010, Dias et al. 2015). Therefore, light-based geolocators provide avenues of research geared towards identifying, for the first time, the distribution and behavior of smaller seabird species during the non-breeding period.

Tropicbirds (Phaethontidae), medium-sized tropical seabirds whose at-sea range is poorly known, are suitable candidates for GLS application. A subspecies of the smallest (mean = 385 grams) species, the White-tailed Tropicbird (*Phaethon lepturus catesbyi*), breeds on islands in the North Atlantic Ocean, including Bermuda, which supports the largest (~3,500 nesting pairs) population of this species in the entire Atlantic (Lee and Walsh-McGehee 2000, Dobson and Madeiros 2009, J. L. Madeiros unpubl. data). In the tropics, this species is an asynchronous breeder, with nesting occurring all year-round (Ramos et al. 2005, Catry et al. 2009a). In contrast, the Bermudian population has a defined breeding season from March to September, with few birds departing as late as November, to unknown non-breeding areas.

Whether White-tailed Tropicbirds exhibit sexual segregation at sea is also unknown. Although pairs forage in loose flocks a few miles offshore from Bermuda, ship sightings suggest this species hunts solitarily while far out at sea, plunge diving

for fish and squid, and avoiding mixed-species flocks (Gross 1912, Catry et al. 2009c, D.B. Wingate unpubl. data). Based on the latter observation, we expected no pelagic segregation between non-breeding male and female tropicbirds. Similarly, the diel activity patterns of this species during the non-breeding period are uncertain. In Bermuda, tropicbirds do feeding visits and courtship flight at nest-sites during the early hours of the day, with activity gradually declining late afternoon and ceasing by nightfall (Gross 1912). If the behavior of breeding tropicbirds matches non-breeding birds, we expected higher activity among non-breeding tropicbirds during the day than night periods.

Our goal is to use GLS loggers to map, for the first time in Atlantic waters, the non-breeding distribution of White-tailed Tropicbirds and to quantify their pelagic activity. More specifically, our objectives were to: (1) identify the pelagic range during the entire non-breeding season, (2) identify late summer, fall-winter, and spring core areas and travel routes between seasons, (3) determine if pelagic sexual segregation occurs among non-breeders and (4) quantify diurnal and nocturnal at-sea behaviors.

3.3 Methods

GLS logger deployment and retrieval

We conducted fieldwork at eight breeding sites in Bermuda (32° 31’ N, 64° 75’ W) with tag deployment and retrieval in 2014 and 2015 respectively (Fig. 3-1). From July to August of 2014, we captured 30 late-nesting adults by carefully removing them from nest-cavities by their bill and placing them inside a cotton weighing bag. To process captured adults, we kept birds inside the weighing bag for the following procedures. We recorded body mass of adults with a 500 gram Pesola spring scale (± 1 gram). We measured length of exposed culmen and tarsus (to ±1 mm) with vernier calipers. We measured flattened wing chord (to ± 1 mm) with a wing chord ruler. We then ringed captured adults with a unique identification incoly metal band (0.5 g) on their right leg. On the left leg, we fitted a plastic Darvic band that was equipped with a single Migrate Tec Intigeo C-65. (1 g) geolocator (< 0.5% of adult body mass; Migrate Technology Ltd). We secured loggers to the darvic band with a combination of a small zip tie, with excess zip tie being cut, and moderate application of quick dry two-part marine epoxy (Amazing GOOP®). The geolocator plus band weighed ~ 2g. Prior to logger deployment, we selected six active loggers at random, zip-tied them onto a low shrub, with no leaves, on Nonsuch Island (G on Fig. 3-1) for 29 days, for the open sky calibration technique as described by Lisovski et al. (2012). Each GLS logger measured the light regimes at this site, each producing a single elevation angle, which we averaged and used as the reference sun angle for all birds (Lisovski et al. 2012).

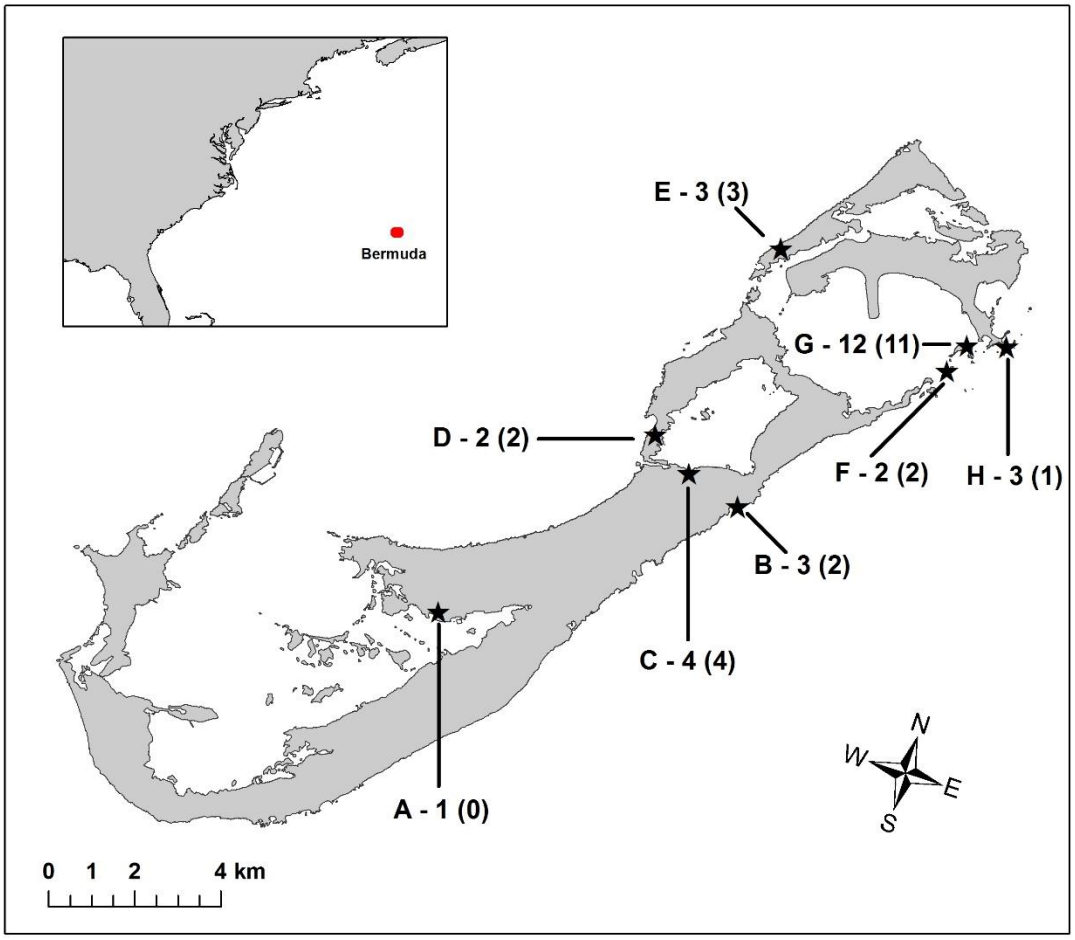


Figure 3-1. Study sites where White-tailed Tropicbirds were captured across Bermuda and fitted with GLS loggers in 2014. Codes for sites: A, Bay House; B, Spittal Pond; C, Bermuda Aquarium; D, Shelly Bay; E, Ferry Reach; F, Horn Rock; G, Nonsuch Island; H, Cooper's Island. Sample sizes for tagged and recaptured birds per site are inside and outside the parentheses respectively.

We kept birds inside the weighing bag until the marine epoxy was dry. Captured adults were either incubating an egg or brooding a chick. Overall handling time was 8-10 minutes. Following processing, we returned adults to their nest-cavities and inserted a towel in the cavity entrance for 5 min to prevent immediate fleeing and give birds time to calm down. We briefly checked adults immediately after towel removal. From April to June 2015, we revisited all sites weekly to remove GLS loggers from recaptured birds. All recaptured birds were weighed and measured following the methodology described above. In addition, we plucked 8 to 10 flank feathers from each recaptured adult and placed samples inside paper envelopes and refrigerated them, until they were analyzed for genetic sex determination at the Genomics and Proteomics Facility at Memorial University of Newfoundland (Fridolfsson and Ellegren 1999).

GLS logger programming and analysis

GLS recorders logged time and light intensity, with estimates of geographic location derived from changes in light intensity across time. Sunrise and sunset events were estimated from thresholds within light curves, with latitude and longitude calculated from day length and time of midday with respect to Coordinated Universal Time respectively (Phillips et al. 2004a).

We obtained raw light data from all geolocators, and imported and viewed each day as light curves within IntiProc v2.0 Geolocation Processing Software from Migrate Technology. We then assigned sunrise and sunset events to each light curve using the auto-mark up command within IntiProc. Since our study focused on birds during the

non-breeding period, all light curves associated with the breeding period were removed. Deep, abrupt dips in light curves were likely caused by birds entering nest-cavities. Therefore, the approximate departure date (i.e., start of the non-breeding period), which varied between individuals (4 July - 8 September), was determined by identifying the last date birds exhibited nest-cavity shading within light curves. Light curves whose sunrise and sunset events were disrupted (i.e., irregular rather than a smooth curve) by cloud cover were identified and removed. We used a sun elevation angle of -7.3° from our averaged calibration data. We further validated this elevation angle by looking at the distributions of birds around Bermuda during the entire breeding season using IntiProc. To account for the natural latitudinal error associated with light-based geolocators, we smoothed validated non-breeding data twice by taking the average of the previous, current, and subsequent position (Phillips et al. 2004a, Fifield et al. 2014). To avoid potential positional errors, fixed start positions (the departure date and return date) for each bird were not smoothed (Phillips et al. 2004a). Latitudes are rendered unreliable around the autumn and spring equinox periods, which resulted in data between 16 September-19 October and 20 February-09 April being removed. The earliest sightings of returning White-tailed Tropicbirds in Bermuda is March, which includes the spring equinox. Although we observed much crevice shading among light curves in March, corresponding to spring sightings in Bermuda, the GLS data of one bird showed crevice-shading post-equinox in April while close to Puerto Rico and the British Virgin Islands, directly south of Bermuda. This suggests some birds may visit crevices in the Caribbean. Without reliable latitudinal data during

the equinox, and Bermuda and Puerto Rico sharing similar longitudes, we cannot confidently determine which island birds are visiting during the spring equinox.

In 2015 we revisited and recorded the contents of all nest-cavities. Tropicbirds whose nest-cavities contained neither egg nor chick upon recapture were considered to be non-breeding adults. Therefore, geolocator data up until the day of recapture was considered as the non-breeding period. If a tropicbird was incubating an egg upon recapture, we estimated approximate egg laying with the hatch date, coupled with crevice shading within IntiProc to determine an approximate end to the non-breeding period.

After IntiProc analysis, non-breeding tracking data was imported into ArcGIS (ESRI, v.10.3.1). The data were projected using the Transverse Mercator Complex projection (Projected Coordinate system: WGS_1984_Complex_UTM_Zone_21N). We generated kernel densities representing the non-breeding locations with Geospatial Modelling Environment (GME) (v. 0.7.4.0; Beyer 2015). In GME we used a raster resolution of 40 km for all kernel densities. We are aware that 50 km is commonly used for seabird geolocation studies (Phillips et al. 2005, Raine et al. 2013, Hedd et al. 2014). However, we used a 40 km cell size strictly for visual purposes of tropicbird distribution, without any environmental layers within our GIS analysis. Lastly, 40 km seemed like an appropriate compromise between considering the spatial error of GLS loggers and capturing key concentration areas. We then used GME to calculate 30, 50, 70 and 90 percent contours for each kernel density in. We defined “core” areas using the 50% contours. We generated kernel densities for the following periods: (1) entire

non-breeding period (July-May); (2) late summer (July-mid-September); (3) fall-winter (late-October-mid-February); and (4) spring (April - May). Lastly, we generated kernel densities representing core ranges of male and female tropicbirds across the non-breeding season.

We set our Migrate Tec C-65 loggers on mode 6, which records periods of saltwater immersion every 30 seconds. The saltwater immersion values ranged from 0 (completely dry) to 20 (completely saturated) and were saved in 10 min intervals for each day. To quantify pelagic activities we manually restored the sunrise and sunset events associated with the breeding season within IntiProc. We then imported the immersion data for each bird into R Studio, where we categorized each day into day and night periods. We calculated the approximate length of day and night for each day from the light curve data. We then used the plot function within R v2.12.1 (R Development Core Team 2010) to graph the average amount of time all birds were dry during the breeding and non-breeding periods. We calculated the average non-breeding pelagic activities of tropicbirds with the non-breeding (July-May) wet and dry data only. To avoid overestimation of dry periods, we removed sunrise and sunset events where birds were clearly inside nest-cavities.

Statistical Analysis

We used paired t-tests to compare mean differences of body mass at initial capture and recapture. We used independent t-tests to compare body mass, bill length, tarsus length and wing chord between recaptured males and females. Lastly, we used independent t-

tests to determine if the pelagic activities of the sexes differed across the non-breeding period. All t-tests were two-tailed and results were considered significant if $P < 0.05$. All statistical tests were run in R (R Development Core Team 2010).

3.4 Results

Retrieval details, body condition and body measurements

Twenty-five (83%) of the 30 breeding birds fitted with GLS loggers in 2014 were recaptured at nest sites in 2015. All 25 loggers recorded data until recapture, which was successfully downloaded for analysis. Birds were lighter during tag deployment than when recaptured ($t = -2.19$, $df = 21$, $P = 0.04$). Males and females did not differ in any body measurements (Table 3-1).

Table 3-1. Descriptive statistics of measurements from recaptured male and female White-tailed Tropicbirds from Bermuda in 2015. Values within parenthesis indicates ranges and sample size.

Variable	Male	Female
Bill length (mm) [a]	49.5 ± 1.97 (46.6 – 52.4; 14)	50.5 ± 2.07 (46.3 – 54.2; 11)
Wing chord (mm)[b]	285 ± 5.8 (274 – 292; 14)	285 ± 8.2 (272 – 302; 11)
Tarsus length (mm) [c]	27.0 ± 1.3 (24.0 – 28.7; 14)	27.5 ± 1.5 (25.1 – 30.0; 11)

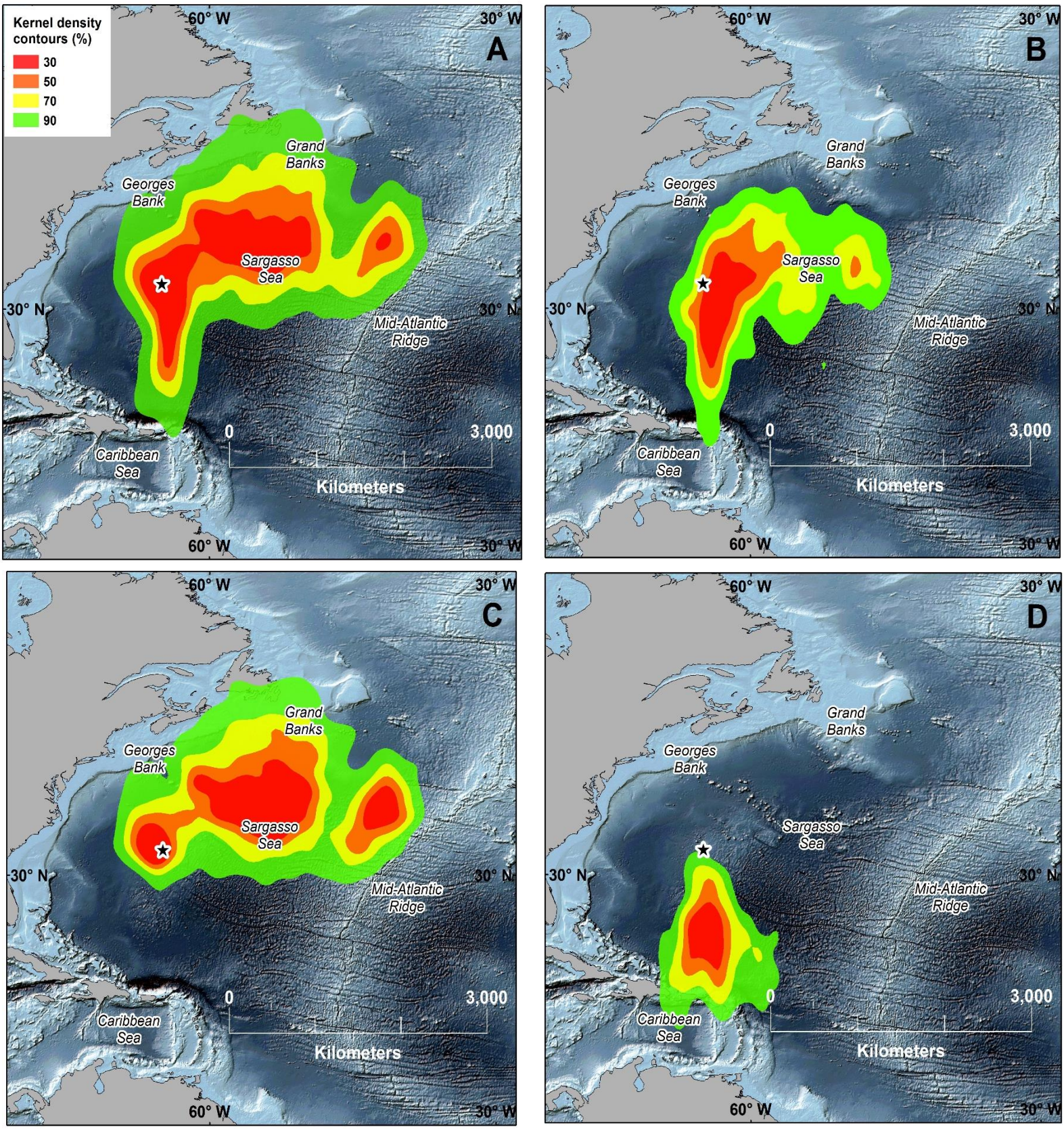
[a] $P = 0.22$ ($t_{21.1} = -1.27$)

[b] $P = 0.72$ ($t_{17.5} = -0.37$)

[c] $P = 0.33$ ($t_{20.3} = -0.99$)

Non-breeding distribution from GLS loggers

During the entire non-breeding period (July-May), tropicbirds were distributed widely across the North Atlantic Ocean (Fig. 3-2a). The full extent of the non-breeding range, as suggested by kernel analysis, extended north to the Grand Banks of Newfoundland, east to the Mid-Atlantic Ridge, south to the British Virgin Islands and west to between Bermuda and North Carolina. Core areas (50% kernels) were concentrated around Bermuda, waters between Bermuda and the Mid-Atlantic Ridge (this boundary hereafter the Sargasso Sea), and the Mid-Atlantic Ridge.


Kernel density contours (%)
30
50
70
90
A
B
C
D
60° W
30° W
30° N
Grand Banks
Georges Bank
Sargasso Sea
Mid-Atlantic Ridge
Caribbean Sea
0
3,000
Kilometers

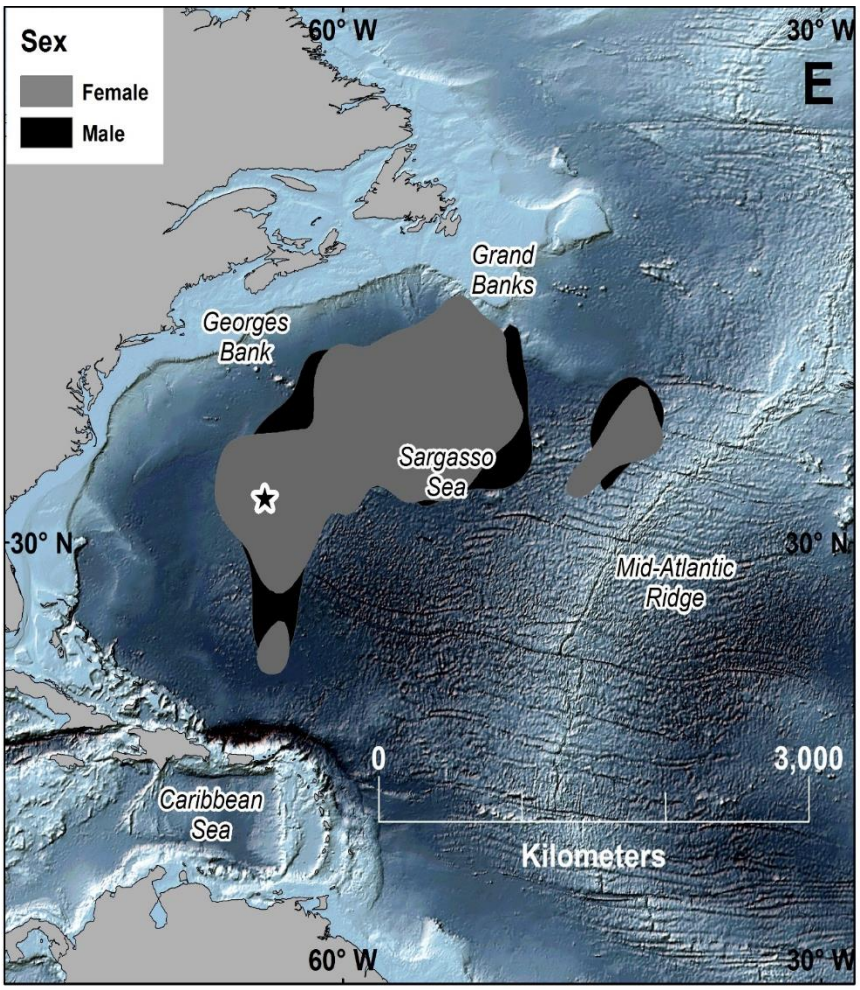


Figure 3-2. Pelagic distribution of 25 White-tailed Tropicbirds from Bermuda (star) during the entire non-breeding period (i.e., from departure to approximate return; A), late-summer period (B), fall-winter period (C), spring period (D) and by sex across the entire non-breeding period (E). Place names mentioned in the text are indicated. Ocean Bottom Layer downloaded from **www.NaturalEarthData.com.**

During the late summer period (July–mid-September) the core area was concentrated around Bermuda (Fig.2b). Eighteen of 25 birds (72%) spent most of the late summer near Bermuda (Table 3-2). Eight birds departed nest sites in July, six of which spent most of that month close to Bermuda, while the other two took a direct easterly route away from the island. August marked the departure of 13 more birds. Eleven of them spent most of August close to Bermuda, while eight individuals flew southward during early and mid-August, reaching northern Puerto Rico. From Puerto Rico, five birds rapidly moved north, returning to Bermuda by the end of August. Fourteen birds, including late departures, flew east from Bermuda by September. By the end of summer, 14 birds were in the Sargasso Sea, three were around the Mid-Atlantic Ridge, six were around Bermuda and two remained close to Puerto Rico.

During the fall and winter period (late-October–mid-February) core areas were concentrated around Bermuda, the Sargasso Sea and the Mid-Atlantic Ridge (Fig. 3-2c). The Sargasso Sea was used heavily by 18 out 25 birds (72%) (Table 3-2). Between late-October and mid-November, 17 (68%) tropicbirds were foraging along the southern Grand Banks of Newfoundland. Tropicbirds at the Grand Banks remained there until mid-November, when 13 flew south into Sargasso Sea and four flew south-east to the ridge. By mid-November, the ridge was being used by 10 birds, two of which flew west, reaching the Sargasso Sea by December. Of the 16 individuals in the Sargasso Sea by mid to late-November, five flew westward, reaching Bermuda by the end of the month. Eight tropicbirds spent December and January in the Sargasso Sea, while three birds used both the Sargasso Sea and Bermudian waters. Eight birds also

remained in the Mid-Atlantic Ridge in December and January. The five late-November arrivals to the island remained there until late January, before two flew eastward, returning to the Sargasso Sea by February. Similarly, all birds at the ridge took a westerly route by late-January, with all individuals returning to the Sargasso Sea by mid-February.

Table 3-2. Summary of movement data on 25 White-tailed Tropicbirds fitted with GLS loggers in Bermuda. For information on dates see text. Late summer (July-September), fall and winter (October-February) and spring (April-May) indicates main waters each bird occupied during those periods. BDA = Bermuda.

GLS No	Sex	Body mass deployment (g)	Body mass retrieval (g)	Late Summer	Fall & Winter	Spring
N391	F	366	No data	BDA	Sargasso, BDA	Southern BDA
N393	F	365	365	BDA	BDA	Caribbean Sea
N394	F	355	365	BDA	Sargasso, BDA	Southern BDA.
N395	M	367	375	BDA	Ridge	Northern Virgin Is.
N396	M	413	395	BDA	Sargasso	Northern Barbuda
N397	M	432	395	BDA	Ridge, Sargasso	Dominican Rep
N398	F	297	390	BDA	Ridge, Sargasso	Northern Barbuda
N399	M	349	390	BDA	Sargasso, BDA	No data
N400	M	397	450	Virgin Is	Ridge	Southern BDA
N402	M	461	405	BDA	Sargasso, BDA	Southern BDA
N730	F	439	465	Sargasso	Ridge	Southern BDA

N733	F	374	350	BDA	Sargasso, BDA	Southern BDA
N734	F	402	405	Virgin Is.	Sargasso	No data
N735	M	407	440	Sargasso	Ridge	Southern BDA
N736	M	391	405	BDA	BDA	Northern Barbuda
N737	M	385	430	BDA	Sargasso, Ridge	Northern Barbuda
N738	F	No data	385	BDA	Ridge, Sargasso	Northern Puerto R
N739	F	304	375	Sargasso	Ridge, Sargasso	Southern BDA
N740	M	349	No data	BDA	Sargasso	Northern Barbuda
N741	F	309	365	BDA	Sargasso, Ridge	Southern BDA
N742	M	391	395	BDA	BDA	Southern BDA
N743	M	361	355	BDA	Ridge, Sargasso	Southern BDA
N745	M	384	365	BDA	Sargasso	Southern BDA
N746	M	347	375	Virgin Is.	Sargasso	Southern BDA
N747	F	392	445	Sargasso	Ridge, Sargasso	Eastern Barbuda

During the spring period (April – May) all tropicbirds were located in a core area between Bermuda and the British Virgin Islands (Fig. 3-2d). Fourteen birds out of 23 (61%) spent the majority of the spring period there (Table 3-2). During early and mid-April, 17 tropicbirds were in the Caribbean Sea, near Hispaniola, Puerto Rico and the British Virgin Islands. The onset of the northern route back to Bermuda began by mid-April, with 16 individuals arriving in Bermuda before the end of April, while 7 birds remained between Bermuda and the British Virgin Islands. In May the remaining birds in the core area completed a northern route to Bermuda. We were unable to determine their precise spring movements of two birds because our nest monitoring data suggests their eggs were laid close to the equinox period.

Distribution of males and females

We recaptured 14 males and 11 females (Table 3-2). Core areas of both sexes in the non-breeding period were concentrated in Bermuda, Sargasso Sea, and the Mid-Atlantic Ridge; ranges of both sexes overlapped extensively (Fig 3-2e).

At-sea activity patterns

We observed distinct patterns in the daily and nightly pelagic activities of birds within and outside the breeding season (Fig. 3-3). During the breeding seasons, birds spent higher percentage of their time dry. This was true for both day and night periods. The start of the non-breeding season is marked by a sharp decline in the percent of time birds were dry, particularly at night (Fig 3-3). This trend persisted for the entirety of the non-breeding period, with the start of the following breeding season beginning with

an abrupt increase in daily and nightly dryness. During the non-breeding period, sexes showed similar pelagic activities during the day and night (Table 3-3). Hereafter, we report results from pooled data, since sexes did not differ ($P > 0.05$ for all t tests). Birds flew more during the day than night (Fig. 3-3). Despite this, all non-breeding birds spent most of the day on the water (59% of time, on average) compared to daily flight (41%) (Table 3-3). All non-breeding birds spent most of the night period on water (95%) (Table 3-3).

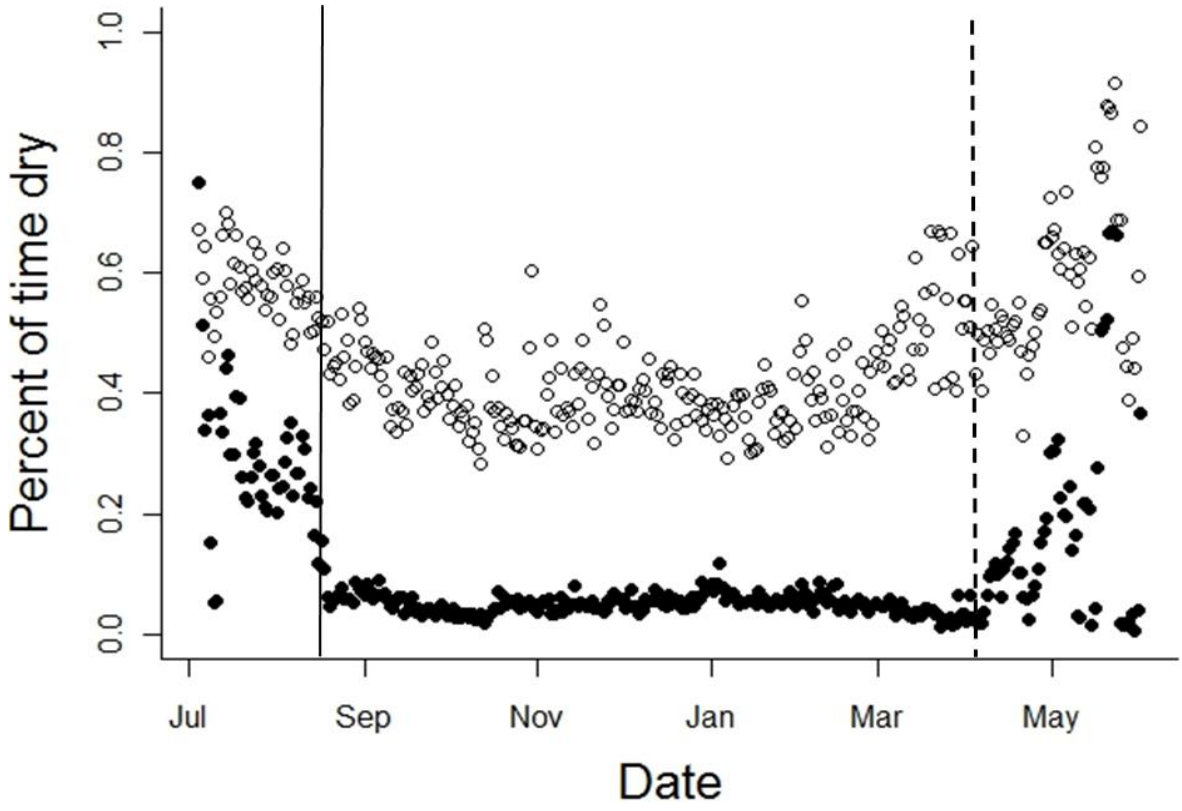


Figure 3-3. Average time 25 tagged White-tailed Tropicbirds were dry during day (hollow circles) and night (dark circles) periods during the breeding and non-breeding period. The approximate start and end of the non-breeding period are denoted with a solid and dashed line respectively. Average percent time dry during day and night periods declined during the non-breeding period and steadily increased during the following breeding period.

Table 3-3. Pelagic activity patterns of 25 White-tailed Tropicbirds recorded from GLS loggers across the non-breeding period. Values are means of individual bird means ± SD with the range of individuals in parenthesis.

	Males	Females	All Non-breeding birds
Time wet (%) during:			
Daylight	0.57 ± 0.07	0.60 ± 0.03	0.59 ± 0.05
	(0.42 - 0.69)	(0.57 - 0.67)	(0.42 - 0.69)
Darkness	0.93 ± 0.03	0.95 ± 0.02	0.95 ± 0.02
	(0.85 - 0.97)	(0.92 - 0.98)	(0.85 - 0.98)
Time flying (%) during:			
Daylight	0.42 ± 0.07	0.40 ± 0.06	0.41 ± 0.06
	(0.30 - 0.57)	(0.32 - 0.57)	(0.30 - 0.57)
Darkness	0.06 ± 0.03	0.04 ± 0.02	0.05 ± 0.02
	(0.02 - 0.14)	(0.01 - 0.07)	(0.01 - 0.14)
Total time wet (h):			
Daylight	6.92 ± 0.85	7.34 ± 0.47	7.10 ± 0.73
	(5.05 - 8.31)	(6.78 - 8.48)	(5.05 – 8.48)
Darkness	11.0 ± 0.5	11.0 ± 0.5	10.9 ± 0.45
	(9.7 - 11.3)	(10.4 - 11.6)	(9.7 – 11.6)
Total time in flight (h):			
Daylight	5.11 ± 0.92	4.78 ± 0.36	4.97 ± 0.73
	(3.67 - 7.13)	(4.05 - 5.22)	(3.67 - 7.13)

Darkness	0.70 ± 0.30	0.51 ± 0.24	0.61 ± 0.29
	(0.30 - 1.43)	(0.17 – 0.83)	(0.17 – 1.43)

3.5 Discussion

We provide the first description of the non-breeding distribution and pelagic activities of a tropicbird species in the Atlantic Ocean. Recaptures of tagged seabirds are often mixed; studies report high (Ismar et al. 2011, Gaston et al. 2011) and low (Phillips et al. 2007, Bustnes et al. 2013, Maftei et al. 2015) geolocator recoveries. We recaptured the majority (83%) of our birds. The high nest-site fidelity of Bermudian White-tailed Tropicbirds, whose nest-cavities limited escape possibilities, benefited recapture. The five birds we failed to recapture were not seen in 2015. It is possible these birds died over the non-breeding period. Survival of White-tailed Tropicbirds on Aride Island was 0.81(Catry et al. 2009a), a percentage closely matching our recovery rate. Alternatively, these birds could have changed nest-cavities. In 2015 we recaptured one adult in a nest-cavity a few meters from the nest-cavity it was using in 2014.

Tropicbird mass at recapture was larger than their mass at tagging. This contrasts with previous seabird studies where mass declined among tagged adults (Nisbet et al. 2011) and chicks (Adams et al. 2009). Seabirds carrying tracking devices may also experience reduced flight efficiency (Passos et al. 2010) and have lower colony attendance (Sohle et al. 2000). However, the return of 25 tropicbirds that began nesting suggests our small devices had minimal effect on carriers.

The first tropicbirds to leave breeding sites in late summer (July-mid-September) lingered around Bermuda. Despite eight birds flying south from Bermuda mid-August, towards northern Puerto Rico, five returned to Bermuda by late-August. This suggests prey, such as the Caribbean reef squid (*Sepioteuthis sepioidea*), Atlantic flying fish

(*Cheilopogon melanurus*) and pufferfish (Tetraodontidae) (MM unpubl. data) were available around Bermuda. However the strong eastern departure of 14 birds in September, regardless of time of colony departure, may mark the decline in foraging conditions.

In the fall and winter period (late-October–mid-February) White-tailed Tropicbirds showed considerable variation in distribution, being found in Bermuda, the Sargasso Sea and the Mid-Atlantic Ridge; a similar distribution as the Bermuda Petrel (*Pterodroma cahow*; Madeiros et al. 2013). Despite being a tropical species, 17 White-tailed Tropicbirds were at the Grand Banks of Newfoundland during late-October and mid-November. The Grand Banks is one of the most nutrient rich zones in the ocean, with significant nutrient upwelling and supports a large number of fish and squid (Anderson and Gardner 1986, Montevecchi and Myers 1995). Such fish densities, in turn, support an estimated 40 million seabirds annually (Montevecchi and Tuck 1987, Lock et al. 1994, Hedd et al. 2012).

Our data matches previous tropicbird sightings in Newfoundland waters. A Red-billed Tropicbird was seen on the Newfoundland Banks in 1876 (Mactavish 2005). Similarly, in 2006, a White-tailed Tropicbird carcass was found in St. John's Newfoundland in mid-September, after a tropical storm (Mactavish 2007). The presence of tropicbirds off Newfoundland is likely explained by the warm subtropical waters of the Gulf Steam, running from the southern tip of Florida to eastern Newfoundland. The large number of Bermudian tropicbirds on the Grand Banks suggests this is an important foraging region for this species in the fall. However, their

prey in these waters are a mystery. Possible prey could be Atlantic saury (*Scomberesox saurus*) and the northern shortfin squid (*Illex illecebrosus*) (Hurley 1980, Dudnick et al. 1981, Perez 1994). Both species can be as small as 20 cm and found along the surface, traits favoring plunge diving by foraging tropicbirds (Squires, 1957, Dudnick et al. 1981, Wigley 1982). Not surpassingly, tropicbird foraging time along the Banks is constrained by temperature. All birds steadily flew southward from the Grand Banks by mid-November, coinciding with the cooling of the area by the Labrador Current.

Five tropicbirds spent most of the fall and winter period in Bermuda, coinciding with rare onshore sightings of this species in December and January. Bermuda is seemingly void of tropicbirds in winter months, but our data indicate small numbers spend much of the non-breeding season in Bermudian waters, likely far offshore. Strong gales dominate Bermuda's winter season, possibly making plunge diving for prey in these waters more difficult. Therefore, the subtropical climate of Bermuda may explain why White-tailed Tropicbirds do not breed aseasonally, as it does in the tropics (Phillips 1987, Diamond 1975).

The waters between Bermuda and the Mid-Atlantic Ridge (the Sargasso Sea), supported the largest concentration of tropicbirds in winter. This area has large patches of floating brown seaweed (*Sargassum spp*.) that supports many prey items for tropicbirds, including the Atlantic flyingfish (Adams 1960, Dooley 1972). The influx of tropicbirds to the Sargasso Sea was apparent by mid-November, after 13 birds flew there from the Grand Banks. Previous ship surveys conducted between 29º

and 32º N, off eastern Florida, found 50% of White-tailed Tropicbirds foraging among *Sargassum spp*. patches (Haney 1986). Therefore, *Sargassum* is a rich resource for foraging tropicbirds in otherwise nutrient-poor waters of the North Atlantic and explains their dense concentration in this area in winter.

Our fall and winter kernel analysis did not reflect some extreme movements displayed by some birds. For example, in late October, five tropicbirds were in the Labrador Sea, two of which were just south of Greenland, before all birds flew south, leaving the Labrador Sea by November. Although the latitudinal error of geolocators could explain these extreme northern distributions, the removal of equinox periods, followed by smoothing reduced this error within our data. Alternatively, strong weather systems could have forced these birds up north. However, tropicbirds were still in the Grand Banks weeks after Hurricane Gonzalo, which first passed over Bermuda October 18th, 2014, and passed the Avalon Peninsula, Newfoundland, mid October. Therefore, our data suggest tropicbird residency in this area was not entirely storm dependent. The longest longitudinal distance seen was one bird in late November flying east, stopping west of the Azores; approximately 2,500 km from Bermuda. This matches the rare sighting of a White-tailed Tropicbird in the Azores in mid-late October (Monticelli and Aalto 2012). Similarly, another bird flew west, reaching North Carolina along the eastern seaboard by late December.

In the spring period (April-May) all non-breeding White-tailed Tropicbirds were between Bermuda and the British Virgin Islands; demonstrating a more localized core area; contrasting their erratic and dispersive movements in the winter. Fourteen birds

(56%) spent majority of their time in waters between Bermuda and the British Virgin Islands. This aggregation of tropicbirds could coincide with when the species becomes more social as the breeding season approaches. Alternatively, these waters may act as a productive, pre-breeding foraging area, as seen with other tropical seabirds (Catry et al. 2009b). Our data also confirm that the Bermudian tropicbird population overlaps with the Caribbean tropicbird population. Ten of 25 birds spent early–mid-Spring close to Puerto Rico, which supports 200-300 nesting White-tailed Tropicbird pairs (Lee and Walsh-McGehee 2000). We also found abrupt dips in our light curve data in one bird, indicating cavity shading, at the time the bird was close to Puerto Rico and the British Virgin Islands in early-April. This suggests Bermudian tropicbirds enter cavities or crevices while in the Caribbean, following resident tropicbirds into their nest sites, a behavior observed among Bermudian breeding sites (M. Mejías unpublished data).

As expected, we found no evidence of pelagic segregation among non-breeding male and female White-tailed Tropicbirds. Both sexes used Bermudian waters and the Sargasso Sea during the entire non-breeding period. Other seabirds have pronounced at-sea segregation between sexes, like the Wandering Albatross (*Diomedea exulans*), Grey-headed Albatross (*Thalassarche chrysostoma*), Black-browed Albatross (*Thalassarche melanophris*) and the Northern Giant Petrel (Phillips et al. 2004b, Xavier et al. 2004, González-Solís et al. 2007). These species exhibit moderate to extreme sexual size dimorphism, allowing one sex to exploit a specific region more effectively than the other. Whereas male and female White-tailed Tropicbirds are

similar sized and likely have similar flight capabilities, and hunt solitarily, which may prevent size behavioral dominance and competition for resources between male and female tropicbirds (Catry et al. 2009c).

The pelagic activities of White-tailed Tropicbirds differed between the breeding and non-breeding periods. Breeders spent higher percentage of day and night periods dry. This was expected because nesting birds regularly visit nest sites. In contrast, the non-breeding season began with an abrupt and consistent trend of birds spending less time dry during both day and night periods. Non-breeders flew more during the day than night. The lack of nocturnal flight was not surprising because tropicbirds hunt by day, detecting prey on the wing by sight, rather than olfactory cues of nocturnal seabirds (Nevitt 1999). Non-breeding tropicbirds spent 41% (5 hours) of day periods in flight. We interpret these long dry periods as foraging effort, where prey is distributed patchily in nutrient poor tropical and subtropical waters, especially when travelling between *Sargassum* seaweed rafts. (Russel-Hunter 1970, Flint 1991). Despite non-breeding birds flying more during daylight, tropicbirds spent higher proportion of day periods wet, suggesting their flight style is energetically expensive, compared to dynamic soaring used by albatrosses, which use wind energy over waves to fly for indefinite periods with minimal flapping (Alerstam et al. 1993, Weimerskirch et al. 1997). All tropicbirds spent darkness predominantly immersed in water, confirming for the first time, that tropicbirds roost on the water surface at night.

We are confident that our wet bout data are reliable estimates of the pelagic activities of White-tailed Tropicbirds. First, although tropicbirds tuck their feet into

their plumage, at least in flight, our loggers consistently recorded birds as mostly saturated during night periods. Lastly, tropicbirds are strictly pelagic outside the breeding season and have small, weak feet that prevent them from perching effectively on buoys, rock outcrops and cliffs. Therefore, we interpret the dry periods observed with our individuals to be indicative of flight.

Conservation Implications

Our study documents, for the first time, waters occupied by a tropicbird species outside of the breeding season in the Atlantic Ocean. Bermudian White-tailed Tropicbirds ranged from the eastern seaboard of the United States to just west of the Azores, with birds varying greatly in movements within this broad area, particularly the winter period. Given Bermuda supports the largest population of White-tailed Tropicbirds (~ 3,500 breeding pairs) in the Atlantic, our movement data have important conservation implications for this species across their annual range. For example, we identified waters where tropicbirds from Bermuda are at risk of oil pollution. In the 1960s Bermudian tropicbirds were seen covered in oil from tar balls spilled into the Sargasso Sea, resulting in mass breeding failure to as late as the 1970s (Butler et al. 1973). This chronic oil exposure was the result of tar balls continuously circulating within the gyre of the Sargasso Sea, where our data indicated tropicbirds spend a large proportion of their time. Tar pollutants have since been greatly reduced within the Sargasso Sea since the 1980s, following stricter shipping policies (Smith and Knap 1985). Although oil

pollutants are currently a reduced threat throughout the core non-breeding areas, we identified specific waters where migratory North Atlantic tropicbirds are vulnerable.

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4. Summary and General Discussion

4.1 Thesis Summary

In this thesis, I have described the important determinants of nest-site selection, nest survival and predation of nesting of Bermudian White-tailed Tropicbirds and their pelagic post-breeding distribution and behaviour. I will first highlight our results from monitoring breeding birds inside natural and artificial cavities, the latter cavity type not used anywhere else for this species. Nest-cavity preferences for White-tailed Tropicbirds differed between birds using natural or artificial cavities. Tropicbirds inside natural cavities preferred those containing nesting sand, with smaller entrances and located on steeper coastal cliffs. Birds using artificial cavities on mainland sites preferred deeper cavities, whereas cavity depth did not affect occupancy of offshore island nesters. Unlike natural cavities or artificial cavities on offshore islands, where no temporal pattern was observed, we found annual variation in occupancy of artificial cavities on the mainland.

Some of these nest-site characteristics affected the survival of tropicbird clutches and nestlings. I found clutch survival was lower in nesting sand containing rubble, and increased inside deeper cavities with smaller entrances. In contrast, nestling survival was unaffected by physical characteristics of cavities. Instead, nestling survival was dependent on temporal factors, with lower survival across years, and declined as the season progressed and increased with nestling age.

Some nest-cavity characteristics and temporal factors affected tropicbird nest predation from Black Rats and American Crows. We found rats preying on tropicbird nest contents, regardless of cavity-type, whereas crows largely targeted natural cavities. We found rat predation was higher on mainland sites, compared to offshore sites. Both rat and crow predation varied temporally, with higher and lower rates occurring respectively across the three year study period. Rats readily ate cavity contents, regardless of cavity dimensions, whereas crows could only access shallower cavities with larger entrances.

To study the non-breeding biology of White-tailed Tropicbirds, I used light-based geolocators to identify, for the first time in Atlantic waters, the entire non-breeding distribution of this species. We retrieved data from 25 recaptured tropicbirds at their breeding sites in Bermuda. My data indicated 72% of Bermudian tropicbirds spent the late-summer period close to Bermuda, before most birds flew eastwards, away from the island, into the Sargasso Sea. We also discovered that wintering tropicbirds from Bermuda disperse widely across the winter period. In the fall and winter period, tropicbirds were found in Bermuda to as far east the Mid-Atlantic Ridge. I also found 68% of tropicbirds relying on the temperate waters along the Grand Banks of Newfoundland in late-October-mid-November. Unlike their winter distribution, all tropicbirds in the spring were concentrated in the same area, gathering in waters between Bermuda and the British Virgin Islands, possibly indicating breeding pairs attempting to reunite at-sea prior to returning to their breeding sites or an extremely

productive foraging area for pre-breeders. From this spring core area, all birds took a northerly route back to their breeding sites in Bermuda during April-May.

After confirming the sex of recaptured tropicbirds (14 males, 11 females) I investigated if non-breeding tropicbirds showed any at-sea sexual segregation, a pattern that has not been previously explored with this species. My data showed that non-breeding males and females used the same waters across the entire non-breeding season. Although males appeared to be skewed slightly to the east, this difference was small.

Lastly, I used the salt water immersion data collected from GLS loggers to quantify the day and night pelagic activities of White-tailed Tropicbirds during the breeding and non-breeding season. During the breeding season, tropicbirds were predominantly drier during day and night periods, when tropicbirds reside at nesting-sites. In contrast, tropicbirds in the non-breeding season were considerably less dry during day and night periods. Although flight was largely confined to daylight, non-breeding tropicbirds spent majority (59%, on average) of their daily activities on water. My data also indicated that tropicbirds were predominately (95%) wet during night periods, confirming this species roosts on the water at night. All of the data from the geolocators provided novel information, filling in large knowledge gaps of the natural history of a non-breeding tropicbird species.

4.2 Limitations

Although my results increased our understandings on the breeding and non-breeding ecology of White-tailed Tropicbirds, both studies have limitations that are worth mentioning. For example, in my nest-cavity selection study I wanted to determine if tropicbird cavity occupancy was influenced by cavity location, presence of nesting sand, cavity depth, entrance height and slope of coastal terrain. Although the natural cavities showed variation in these traits, the artificial cavities only differed in location and cavity depth, thus limiting the variables I could test. However, all of the artificial cavities contained nesting sand, had smaller entrances and were located on steep coastal cliffs, all of which were important determinants of natural cavity occupancy. Nonetheless, having variation among recorded variables is important because possible determinants of cavity occupancy can differ between natural and artificial cavities.

I also did not take into account that the artificial cavities in my study were installed at various times, some even years apart. Older cavities could have higher occupancy than newer cavities, because they have been around longer for birds to eventually find them. However, I do not suspect this to be a major factor in my system because when the artificial cavities among the densest colonies on the Castle Harbor Islands were newly installed, they were occupied the same season of installment; whereas the few mainland cavities that are of similar age installed on mainland sites, which had fewer tropicbirds, took longer to colonize. Therefore, rather than the actual age of artificial cavities, the distance an artificial cavity is from a source population, a

factor not considered in this study, is likely a more important factor driving artificial cavity occupancy.

Another limitation was the relatively large gaps in my nest-cavity checks in 2013 and 2014, when I checked mainland and offshore cavities fortnightly and every third week respectively. Consequently, this sampling regime resulted in greater uncertainty in the timing of clutch and nestlings failures, as well as fledging dates. Increasing the sampling of mainland and offshore sites to once and twice a week respectively improved my confirmation of nest-cavity fates. Despite annual differences in the sampling regime, some trends, like high nestling high mortality during the first few weeks of life, was consistent in all three years. Regardless, I would highly recommend those conducting similar studies in the future to monitor nest-cavities as frequently as possible.

For our non-breeding distribution study, the most obvious limitation is the average error (186 ± 114 km) in the accuracy of light-based geolocators. Although several data analysis techniques exist to reduce the inherent "noise" with geolocators, other complimentary data could further validate such tracking data. For example, due to limitations in device settings, the geolocators we used were not programmed to record sea surface temperature, which would have strengthened some of the more northern extreme sightings we observed with tropicbirds. Other researchers used stable isotope analysis in addition to geolocator data, to infer the wintering areas of seabirds (Militao et al. 2013, Pérez et al. 2014). Stable isotope analysis on feathers can indicate prey eaten by seabirds while occupying specific areas, which can be matched to areas

geolocators place birds (Quillfeldt et al. 2005). However, there is uncertainty on when White-tailed Tropicbirds undergoes a full molt. Lastly, due to their reliance on sun angles, geolocator data becomes very unreliable during spring and autumn equinox periods. This results in the removal of 3-4 weeks of data around September-October and March, resulting in unknown locations in those timeframes. Small (1.6 g), satellite tags, albeit expensive, would remedy this problem. Despite their inherent latitudinal limitations, light-based geolocators are relatively inexpensive devices whose large error in accuracy is relatively minuscule at the global extent and is thus very effective in tracking large scale movements of non-breeding seabirds.

4.3 Conservation Implications

To protect a highly migratory species, it is important to understand nest-site characteristics that affect their reproduction, identify where post-breeders disperse and how they behave during this period. My results highlight important determinants of nest survival and, for the first time, the non-breeding whereabouts and daily pelagic activities of White-tailed Tropicbirds in the North Atlantic.

Implications for breeding White-tailed Tropicbirds

My results suggest that providing artificial cavities for breeding White-tailed Tropicbirds can be beneficial to the entire nesting population. Although artificial cavities did not improve or hinder the breeding success of tropicbirds, compared to natural cavities, they provided additional breeding sites in areas where nest-cavities

were limited. We found the occupancy of mainland artificial cavities steadily increased across the study period, as has been seen elsewhere with European Storm-Petrels (de León and Mínguez 2003). In the context of this study, I observed tropicbirds showing a preference for a specific cavity trait in one location but not in the other. More specifically, mainland nesters preferred deeper artificial cavities whereas cavity depth did not affect artificial cavity occupancy of offshore nesters. I believe this difference is the result of mainland sites having a higher abundance of mammalian predators compared to offshore sites, which is generally free of such predators. The location of artificial cavity installation is known to influence their occupancy, particularly with land birds (Rendell and Robertson 1989, White et al. 2006). Therefore, I recommend seabird biologists to take a similar approach and consider differences in habitat quality between locations, before installing artificial cavities, in hopes of having high occupancy among all artificial cavities installed.

Although tropicbirds nesting on offshore islands readily accepted shallower artificial cavities, we would still recommend making these cavities deeper because shallower cavities leave breeders vulnerable to avian predators, as seen with crows in this study and Yellow-legged Gulls preying on nesting petrels in Benidorm (Oro et al. 2005).

Most seabirds, including tropicbirds, have strong nest-site fidelity and will continue to use nest sites that reduce breeding success, making them prone to ecological traps (Igual et al. 2007, Reynolds et al. 2015). In the context of this study, I found nest-cavities with rubble in nesting sand caused significant clutch loss, as seen

with the Madeiran Storm-Petrel (Bolton et al. 2004). Although seemingly minute, egg damage from stones is problematic because most seabirds lay single egg clutches that are not replaced (Cody 1966, Lack 1968). This, coupled with their strong nest-site fidelity, can lower their long-term reproductive output. This places greater emphasis on conservationists to provide managed seabird taxa with nest-cavities free of small stones and preferably deeper cavities, especially if their species is indifferent to cavity dimensions.

Although I found nest-cavity dimensions, including smaller entrance heights, effectively reduced predation from avian predators, their benefits were ineffective against small, mammalian predators, such as Black Rats. Rats are common predators of seabird eggs, chicks and adults on many remote oceanic islands. Their strong negative effect on breeding tropicbirds was very evident after a short two year presence on some offshore islands in Bermuda. The only way to remove such predators is with strategic culling programs (Taylor et al. 2000, Jones 2010). The recovery of nesting seabirds can sometimes can be apparent immediately following the removal of mammalian and avian predators (Lock 2006, Pascal et al. 2008, Sanz-Aguilar et al. 2009). In this study system, I observed a severe decline in crow predation, coinciding with culling effort, across the three year study period. However, this murder of crows was comprised of 8-10 specialized individuals. Nonetheless, my findings suggests seabird biologists should simultaneously build nest-cavities with dimensions that exclude larger predators, while practicing selective removal and increased biosecurity to manage introduced predators, in order to increase seabird breeding success.

Implications for non-breeding White-tailed Tropicbirds at-sea

My results successfully identified the non-breeding movements of White-tailed Tropicbirds in the North Atlantic. Identifying waters used by seabirds outside the breeding season is important because mortality is often higher during this period (Harris et al. 1994). Post-breeding seabirds may leave jurisdictional areas with protection and wander into places where they may encounter pelagic threats such as longline fishing. In the case of Bermudian tropicbirds, we discovered non-breeders using northern temperate waters along the southern Grand Banks of Newfoundland during early winter. Although this region has some oil and gas production and exploration platforms, these activities currently occur to a much lesser extent than in other regions like the Gulf of Mexico (Fraser et al. 2006, Burke et al. 2012). Nonetheless, the few birds that venture to the Grand Banks might be exposed to oil contaminants floating on the water or attracted to artificial night lighting of platforms (Wiese and Ryan 2003, Montevecchi 2006). White-tailed Tropicbird birds are also known to be attracted to vessels at-sea, following them for long periods (Spear and Ainley 2005, MM unpubl. data). Although there could be minimal risk due to the low number of oil platforms in the area, tropicbirds could still be attracted to these gas fields, which could incinerate seabirds that get too close (Ronconi et al. 2015).

Despite our geolocator data indicating tropicbirds retreating south from the Grand Banks, into the Sargasso Sea by mid-November, they are by no means safe from oil pollutants. In the 1970s, many Bermudan tropicbirds were seen returning to breeding sites, with their plumaged fouled in oil, reducing their breeding success during this

time (Lee and Walsh-McGhee 2000). It was speculated the oil was deposited into the Sargasso Sea, where my data indicated tropicbirds spent majority of their non-breeding period. My wet bout data collected from the geolocators revealed, for the first time, that non-breeding tropicbirds spend most of their day and night periods immersed in water. Given this behavior, it is not surprising most tropicbirds seen in Bermuda were covered in oil. Lastly, I determined that both male and female tropicbirds showed a high degree of overlap in pelagic wintering areas. This suggests both sexes from the Bermudian population are likely to encounter and suffer threats with equal probability and magnitude, unlike Wandering Albatross and Flesh-footed Shearwater where sex-specific threats were apparent (Weimerskirch and Jouventin 1987, Gales et al. 1998). Nonetheless, there does not appear to be any obvious at-sea threats currently affecting White-tailed Tropicbirds from Bermuda. However, now that we better understand their post-breeding movements, we can readily investigate specific areas in the event adult return rates to the island are low.

4.4 Future Research Directions

There is still room for additional research on the nesting biology of White-tailed Tropicbirds. Availability of nest sites is often cited as a limiting factor and cause of antagonistic interactions tropicbird colonies, like Puerto Rico (Schaffner 1990), Culebra and the Lesser Antilles (Lee and Walsh-McGhee 2000). In my study, I found that artificial cavities are readily accepted by nesting tropicbirds, especially on island sites where high occupancy suggest limited nest sites, and that that the breeding

success is on par with natural cavities. Given my results, conservationists should consider installing artificial cavities among tropicbird colonies, in the Caribbean. A proxy of the effectiveness of the artificial cavities would be to determine if antagonistic interactions between tropicbirds decline post-artificial cavity installment. Another aspect of nest-site selection and survival that was not addressed in my thesis was the effect of nest-cavity temperature. Temperature is often cited as important determinant of nest-site selection and survival among cavity-nesting birds (Hooge et al. 1999, Wiebe et al. 2001, Rauter et al. 2002). It would be worth comparing daily temperature regimes between natural and artificial cavities and determine if temperature is related to cavity occupancy and survival, as seen with other cavity-nesters. A third research avenue, particularly with Bermuda's population, can access specific nest-site characteristics of cavities most vulnerable to hurricane destruction, a severe threat to Bermuda's population. Potential factors that may be important could be cavity type, elevation above sea level, slope of the coastal terrain, orientation and distance from the ocean. The results of this study may help managers and homeowners alike in accessing ideal places to install artificial cavities that are less likely to be destroyed in violent storms.

Similarly, my tropicbird movement data create new questions, leading to multiple avenues for future research. For example, in the spring period, tagged tropicbirds were shown to forage among the Caribbean islands of Hispaniola, Puerto Rico and the British Virgin Islands, confirming the Bermudian population intermingles with the Caribbean population. With this new information, it would be interesting to fit White-

tailed Tropicbirds from the Caribbean with geolocators to determine if birds there travel to Bermuda. Not only could we determine if birds from the two populations are travelling to foreign islands but also if there is any genetic similarities between the populations. Similar genetic work between distinct populations of the same species have been done with other seabird, such as the Cory's Shearwater, Little Auk (*Alle alle*) and Thick-billed Murre (Birt-Friesen 1992, Rabouam et al. 2000, Wojczulanis-Jakubas et al. 2014). Such a study on tropicbirds could determine if the Bermudian population originated from the Caribbean or vice versa.

Tracking studies can be conducted on juvenile White-tailed Tropicbirds from Bermuda. Band recoveries indicate the age at first breeding is 3 years old (J. L. Madeiros and M. A. Mejías, unpubl. data). It would be useful to know if the distribution of fledgling tropicbirds differ from the range of non-breeding adults. Although geolocators could easily be attached to fledgling tropicbirds, it would be difficult recapture the birds because they would not have established a nest-cavity upon their return to Bermuda 3 years later. Therefore, an alternative would be use smaller satellite tags, where movement can be downloaded from tags, without ever recapturing the bird.

Although I found nest-site selection and nest success patterns at work among Bermuda's breeding population, as well as identified the non-breeding distribution of these birds, my thesis looked at both of these aspects independently. Now that we understand some determinants of tropicbird breeding biology and that geolocators are an effective tool in tracking their post-breeding movements, future research can look

for relationships between tropicbird breeding and non-breeding biology. For example, researchers can test hypotheses linking quality of breeding nest sites and the pelagic distribution of non-breeding tropicbirds. There could be a relationship between where successful and unsuccessful breeders spend the non-breeding season and their respective return dates and the quality of nest-cavities and location they occupy. A study on post-breeding Black-legged Kittiwake (*Rissa tridactyla*) found that successful and unsuccessful breeders showed significant differences in their pelagic distribution (Bogdanova et al. 2011). The ever-evolving improvements of tracking technology, combined with the vast knowledge on seabird breeding biology, allow researchers to pursue finer grained questions of seabirds, both inside and outside the breeding season.

4.5 Literature Cited

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Appendix 1 – White-tailed Tropicbird nest-cavity monitoring data from 2013-2015. These data represents the contents of all nest-cavities during my last visit for each year. Data includes study sites (site abbreviations: BA = Bermuda Aquarium, BI = Bay Island, BH = Bay House, CI = Cockroach Island, Cis = Cooper's Island, DH = Daniel's Head, FR = Ferry Reach, GI = Gamma Island, HR = Horn Rock, LI = Lambda Island, LR = Long Rock, NI = Nonsuch Island, PI = Pearl Island, RI = Rabbit Island, RIs = Rickett's Island, SB = Shelly Bay, SI = Southampton Island and SP = Spittal Pond), nest-cavity number (C#), nest-cavity type (CT; A = artificial, N = natural), location (L; M = mainland, I = island), substrate presence (SP; S = substrate, NS = no substrate), rubble presence (RP; R = rubble, NR = no rubble), entrance height (EH; cm), cavity depth (CD; cm), coastal slope (CS), neighbor numbers (NN), date (year/month/day) and nest-cavity fate (CF; EM = empty cavity). See tropicbird nestling plates below to refer to specific chick age classes mentioned in nest-cavity fate column. Note, 2013 does not have detailed chick developmental stages specified.

Sites	C#	CT	L	SP	RP	EH	CD	CS	NN	Date	CF
BA	1	A	M	S	R	12.7	60.96	15.77	NA	2015-08-28	EM
BA	2	A	M	S	R	20.32	85.09	15.72	0	2015-08-28	Egg2broke
BA	3	A	M	S	NR	12.7	74.93	10.74	0	2015-08-28	Fledged
BA	4	A	M	S	R	12.7	49.53	23.43	0	2015-08-28	Midfledgedchick
BH	1	A	M	S	R	21.59	109.22	40.03	2	2015-08-28	EM
BH	2	A	M	S	NR	27.94	113.03	40.03	3	2015-08-28	Midscapchick
BH	3	A	M	S	R	17.78	111.76	40.03	2	2015-08-28	Halffledgedchick
BH	4	A	M	S	R	20.32	109.855	40.03	1	2015-08-28	RatPredation
BH	5	A	M	S	NR	16.51	119.38	40.03	1	2015-08-28	Fledged
BH	6	A	M	S	R	15.24	114.3	40.03	3	2015-08-28	Fledged
BH	7	A	M	S	R	12.7	121.92	40.03	3	2015-08-28	Fledged
BH	8	A	M	S	R	20.32	124.46	40.03	2	2015-08-28	Fledged

BH	9	A	M	S	R	15.24	119.38	40.03	3	2015-08-28	Fledged
BH	10	A	M	S	R	12.7	165.1	40.03	2	2015-08-28	Fledged
BH	11	A	M	S	R	15.24	139.7	40.03	1	2015-08-28	Fledged
BH	12	A	M	S	R	16.51	152.4	40.03	NA	2015-08-28	EM
BH	13	A	M	S	R	34.29	139.7	40.03	NA	2015-08-28	EM
BH	14	A	M	S	NR	33.02	138.43	40.03	1	2015-08-28	Fledged
BH	15	A	M	S	NA	22.86	137.16	40.03	2	2015-08-28	Fledged
BH	16	A	M	S	NR	27.94	127	40.03	1	2015-08-28	Fledged
BH	17	A	M	S	NR	11.43	124.46	40.03	1	2015-08-28	FullyFledgedchick
BH	18	A	M	S	R	22.86	104.14	40.03	2	2015-08-28	Fledged
BH	19	A	M	S	NR	16.51	72.39	40.03	1	2015-08-28	Fledged
BH	20	A	M	S	NR	15.24	71.12	40.03	NA	2015-08-28	EM
BH	21	A	M	S	NR	17.78	71.12	40.03	NA	2015-08-28	EM
BH	22	A	M	S	NR	16.51	74.93	40.03	NA	2015-08-28	EM
BH	23	A	M	S	NR	15.24	66.04	40.03	NA	2015-08-28	EM
BH	24	A	M	S	R	16.51	64.77	40.03	2	2015-08-28	RatPredation
BH	25	A	M	S	NR	16.51	69.85	40.03	NA	2015-08-28	EM
BH	26	A	M	S	NR	17.78	71.12	40.03	NA	2015-08-28	EM
BH	27	A	M	S	NR	16.51	67.31	40.03	NA	2015-08-28	EM
BH	28	A	M	S	NR	15.24	64.77	40.03	NA	2015-08-28	EM
BH	29	A	M	S	NR	15.24	79.24	40.03	NA	2015-08-28	EM
BH	30	A	M	S	R	17.78	67.31	40.03	NA	2015-08-28	EM

BH	31	A	M	S	R	20.32	64.77	40.03	NA	2015-08-28	EM
BH	32	A	M	S	NR	20.32	64.77	40.03	NA	2015-08-28	EM
BH	33	A	M	S	NR	19.05	77.47	40.03	NA	2015-08-28	EM
BH	34	A	M	S	NR	17.78	63.5	40.03	3	2015-08-28	RatPredation
BH	34	A	M	S	NR	17.78	63.5	40.03	3	2015-08-28	RatPredation
BH	35	A	M	S	NR	17.78	71.12	40.03	NA	2015-08-28	EM
BH	36	A	M	S	NR	16.51	68.58	40.03	NA	2015-08-28	EM
BH	37	A	M	S	NR	16.51	66.04	40.03	NA	2015-08-28	EM
BH	38	A	M	S	R	13.97	68.58	40.03	NA	2015-08-28	EM
BH	39	A	M	S	R	17.78	72.39	40.03	NA	2015-08-28	EM
BH	40	A	M	S	NR	27.94	73.66	40.03	NA	2015-08-28	EM
BH	41	A	M	S	NR	15.875	77.47	40.03	NA	2015-08-28	EM
BH	42	A	M	S	NR	16.51	80.01	40.03	NA	2015-08-28	EM
BH	43	A	M	S	NR	16.51	62.23	40.03	1	2015-08-28	Middownychick
CI	1	A	I	S	NR	11.43	73.66	NA	1	2015-07-25	Midfledgedchick
CI	2	A	I	S	R	15.24	55.88	NA	1	2015-07-25	AdultEarlydowneychick
CIs	1	A	M	S	NR	22.86	76.2	17.97	1	2015-08-19	Fledged
CIs	2	A	M	S	NR	15.24	63.5	31.97	1	2015-08-19	Eggbroke
CIs	3	A	M	NS	R	13.97	53.34	48.69	0	2015-08-19	Egg2Abandoned
CIs	4	A	M	S	NR	15.24	63.5	30.56	1	2015-08-19	Fledged
CIs	4A	A	M	S	NR	16.51	66.04	12.95	0	2015-08-19	DeadHatchling
CIs	4B	A	M	S	R	13.97	66.04	36.14	0	2015-08-19	EM

CIs	4C	A	M	S	R	20.32	60.96	30.04	NA	2015-08-19	EM
CIs	4D	A	M	S	R	16.51	69.85	22.02	NA	2015-08-19	EM
CIs	5	A	M	S	R	20.32	66.04	0.00	NA	2015-08-19	EM
CIs	6	A	M	S	R	12.7	60.96	26.41	0	2015-08-19	DeadEarlydownychick
CIs	7	A	M	S	R	12.7	63.5	28.83	NA	2015-08-19	EM
CIs	8	A	M	S	R	15.24	55.88	1.00	NA	2015-08-19	EM
CIs	9	A	M	S	NR	17.78	63.5	0.24	0	2015-08-19	Midfledgedchick
CIs	10	A	M	S	R	15.24	63.5	0.13	0	2015-08-19	Fledged
CIs	11	A	M	S	R	17.78	62.23	17.54	0	2015-08-19	DeadEarlydownychick
CIs	12	A	M	S	R	12.7	63.5	35.69	NA	2015-08-19	EM
CIs	13	N	M	S	R	25.4	71.12	47.67	0	2015-08-19	Earlyscapchick
CIs	14	A	M	S	R	15.24	66.04	35.29	NA	2015-08-19	EM
CIs	15	A	M	S	R	20.32	62.23	32.37	NA	2015-08-19	EM
CIs	16	A	M	S	R	17.78	60.96	44.17	NA	2015-08-19	EM
CIs	17	A	M	S	R	12.7	63.5	35.33	NA	2015-08-19	EM
CIs	18	A	M	S	NR	16.51	59.69	22.15	NA	2015-08-19	EM
CIs	19	N	M	S	NR	16.51	96.52	37.48	0	2015-08-19	Midfledgedchick
CIs	20	A	M	S	R	15.24	76.2	14.99	NA	2015-08-19	EM
CIs	21	A	M	S	R	12.7	66.04	31.30	NA	2015-08-19	EM
CIs	22	A	M	S	NR	15.24	63.5	38.62	NA	2015-08-19	EM
CIs	23	A	M	S	R	16.51	60.96	27.58	NA	2015-08-19	EM
CIs	24	A	M	S	R	15.24	57.15	11.54	NA	2015-08-19	EM

CIs	25	A	M	S	R	15.24	54.61	30.01	0	2015-08-19	DeadEarlydownychick
CIs	26	A	M	S	R	15.24	67.31	32.77	NA	2015-08-19	EM
CIs	27	A	M	S	R	15.24	66.04	24.10	NA	2015-08-19	EM
CIs	28	A	M	S	R	12.7	55.88	29.22	NA	2015-08-19	EM
DH	1	A	M	S	R	13.97	104.14	30.98	0	2015-07-29	Egg2broke
DH	2	A	M	S	NA	16.51	104.14	30.98	NA	2015-07-29	EM
DH	3	A	M	S	NA	15.24	114.3	30.98	0	2015-07-29	EM
DH	4	A	M	S	NA	16.51	129.54	29.93	0	2015-07-29	Fledged
DH	5	A	M	S	NA	17.78	134.62	41.68	NA	2015-07-29	EM
DH	6	A	M	S	NA	20.532	129.54	42.08	0	2015-07-29	EM
DH	7	A	M	S	NA	12.7	111.76	34.46	0	2015-07-29	Fledged
DH	8	A	M	S	NR	12.7	111.76	34.70	NA	2015-07-29	EM
DH	9	A	M	S	R	13.97	107.95	34.70	NA	2015-07-29	EM
DH	10	A	M	S	NR	15.24	110.49	34.70	0	2015-07-29	RatPredation
DH	11	A	M	S	NR	12.7	96.52	34.70	NA	2015-07-29	EM
DH	12	A	M	S	NR	15.24	105.41	15.29	0	2015-07-29	Adult
DH	13	A	M	S	R	16.51	93.98	28.46	0	2015-07-29	Eggbroke
DH	1	N	M	S	NR	38.1	69.85	29.06	0	2015-07-29	EM
DH	2	N	M	S	NR	16.51	113.03	24.60	0	2015-07-29	AdultEgg2
FR	1	N	M	S	NR	17.78	259.08	36.61	NA	2015-08-28	EM
FR	2	N	M	S	NR	30.48	55.88	36.70	NA	2015-08-28	EM
FR	3	N	M	S	NA	40.64	104.14	44.37	0	2015-08-28	Fledged

FR	4	N	M	S	NA	30.48	182.88	45.66	NA	2015-08-28	EM
FR	5	N	M	S	NA	24.765	164.465	27.03	0	2015-08-28	Eggbroke
FR	6	N	M	NS	NR	63.5	60.96	11.79	NA	2015-08-28	EM
FR	6A	N	M	S	NR	40.64	97.79	24.59	0	2015-08-28	Latescapchick
FR	6B	N	M	S	NR	35.56	30.48	19.28	0	2015-08-28	Fledged
FR	6C	N	M	S	NR	22.225	54.61	13.01	NA	2015-08-28	EM
FR	6D	N	M	NS	R	25.4	54.61	18.72	NA	2015-08-28	EM
FR	6E	N	M	S	R	26.67	100.33	19.02	NA	2015-08-28	EM
FR	6F	N	M	S	R	27.94	74.93	20.76	0	2015-08-28	Hatchling
FR	7	N	M	S	R	12.7	81.28	26.47	0	2015-08-28	Fledged
FR	7A	N	M	NS	R	31.75	129.54	34.41	NA	2015-08-28	EM
FR	7A1	N	M	NS	R	27.94	127	27.42	NA	2015-08-28	EM
FR	7B	N	M	NS	NR	25.4	76.2	20.50	NA	2015-08-28	EM
FR	8	N	M	S	NR	15.24	86.36	23.60	0	2015-08-28	Egg2Abandoned
FR	8A	N	M	NS	NR	33.02	58.42	24.38	NA	2015-08-28	EM
FR	9	N	M	S	R	31.75	74.93	20.89	NA	2015-08-28	EM
FR	10	N	M	S	R	12.7	83.82	49.00	2	2015-08-28	Earlyfledgedchick
FR	10A	N	M	S	R	16.51	63.5	48.47	2	2015-08-28	Earlyfledgedchick
FR	10B	N	M	S	NA	17.78	128.27	48.47	NA	2015-08-28	EM
FR	11	N	M	S	NR	19.05	91.44	22.90	0	2015-08-28	Fledged
FR	11A	N	M	S	NR	25.4	63.5	30.64	NA	2015-08-28	EM
FR	11B	N	M	S	NR	30.48	101.6	15.63	NA	2015-08-28	EM

FR	11C	N	M	S	NR	17.78	52.07	13.65	NA	2015-08-28	EM
FR	12	N	M	S	NR	25.4	68.58	9.52	NA	2015-08-28	EM
FR	13	N	M	S	NR	20.32	123.19	12.48	0	2015-08-28	EM
FR	13A	N	M	S	R	27.94	72.39	13.79	NA	2015-08-28	EM
FR	14	N	M	NS	NR	21.59	71.12	43.15	NA	2015-08-28	EM
FR	14A	N	M	NS	NR	15.24	53.34	32.96	NA	2015-08-28	EM
FR	15	N	M	S	NR	22.86	58.42	14.87	NA	2015-08-28	EM
FR	16	N	M	S	NR	48.26	78.74	18.56	NA	2015-08-28	EM
FR	16A	N	M	S	NR	45.72	87.63	17.33	NA	2015-08-28	EM
FR	16B	N	M	S	NR	17.78	38.1	20.28	NA	2015-08-28	EM
FR	17	N	M	S	R	45.72	91.44	35.40	0	2015-08-28	Eggbroke
FR	18	N	M	S	R	10.16	55.88	27.71	3	2015-08-28	Earlyfledgedchick
FR	19	N	M	S	NR	29.21	91.44	27.71	NA	2015-08-28	EM
FR	20	N	M	S	R	39.37	127	27.71	2	2015-08-28	Earlyfledgedchick
FR	21	N	M	S	R	29.21	50.8	27.15	2	2015-08-28	Fledged
FR	22	N	M	S	NR	27.94	86.36	34.33	0	2015-08-28	Fledged
FR	22A	N	M	S	NR	19.05	71.12	15.83	NA	2015-08-28	EM
FR	23	N	M	S	R	22.86	66.04	13.52	NA	2015-08-28	EM
FR	24	N	M	S	R	22.86	60.96	14.30	0	2015-08-28	Eggbroke
FR	24A	N	M	S	NA	41.91	114.3	23.07	NA	2015-08-28	EM
FR	24B	N	M	S	NR	22.86	181.61	31.91	0	2015-08-28	RatPredation
FR	24C	N	M	S	R	34.29	76.2	15.08	0	2015-08-28	DiedWhileHatching

FR	24D	N	M	S	R	17.78	71.12	23.93	0	2015-08-28	Midscapchick
FR	24E	N	M	S	NR	17.78	60.96	5.68	NA	2015-08-28	EM
FR	25	N	M	S	R	27.94	113.03	39.05	0	2015-08-28	RatPredation
GI	1	A	I	S	NR	25.4	76.2	NA	NA	2015-07-07	EM
GI	2	A	I	S	R	20.32	76.2	NA	1	2015-07-07	Adult
GI	3	A	I	S	R	15.24	67.31	NA	1	2015-07-07	DeadEarlydownychick
GI	4	A	I	S	NR	19.05	67.31	NA	NA	2015-07-07	Adult
GI	5	N	I	S	NR	19.05	40.64	27.70	0	2015-07-07	Midfledgedchick
HR	265	N	I	S	R	30.48	58.42	38.60	2	2015-07-29	Fledged
HR	263	N	I	S	R	17.78	55.88	39.92	NA	2015-07-29	EM
HR	262	A	I	S	NR	12.7	78.74	39.92	2	2015-07-29	Halffledgedchick
HR	205	N	I	S	NR	25.4	69.85	29.49	1	2015-07-29	CrowPredation
HR	1	N	I	S	R	20.32	48.26	37.40	3	2015-07-29	Fledged
HR	268	N	I	S	NR	22.86	59.69	24.57	0	2015-07-29	FullyFledgedchick
HR	269A	N	I	S	R	38.1	114.3	24.20	NA	2015-07-29	EM
HR	269	A	I	S	R	27.94	133.35	28.19	NA	2015-07-29	EM
HR	270	A	I	S	NR	17.78	68.58	28.77	0	2015-07-29	FullyFledgedchick
HR	271	A	I	S	R	21.59	71.12	24.84	0	2015-07-29	FullyFledgedchick
HR	273	A	I	S	NR	13.97	66.04	22.35	1	2015-07-29	Eggbroke
HR	274	A	I	S	R	10.16	59.69	27.59	1	2015-07-29	CrowPredation
HR	283	A	I	S	NR	11.43	63.5	29.53	NA	2015-07-29	Adult
HR	282	A	I	S	NR	10.16	63.5	21.84	0	2015-07-29	Adultegg

HR	279	N	I	S	R	27.94	60.96	19.82	NA	2015-07-29	EM
HR	1A	N	I	S	R	33.02	78.74	24.04	1	2015-07-29	Eggbroke
HR	1B	N	I	S	NR	20.32	40.64	25.48	1	2015-07-29	CrowPredation
LI	1	A	I	S	R	10.16	55.88	NA	1	2015-07-07	Halffledgedchick
LI	2	A	I	S	R	10.16	71.12	NA	1	2015-07-07	Midscapchick
LI	3	A	I	S	NR	7.62	58.42	NA	0	2015-07-07	Midscapchick
LR	16	A	I	S	NR	13.97	32.08	6.67	1	2015-07-22	Halffledgedchick
LR	14	A	I	S	NA	12.7	147.32	6.67	NA	2015-07-22	EM
LR	12	A	I	S	NR	12.7	203.2	6.51	1	2015-07-22	FullyFledgedchick
LR	1	N	I	S	NA	15.875	115.57	9.05	NA	2015-07-22	EM
LR	5	N	I	S	NA	17.78	76.2	NA	NA	2015-07-22	EM
LR	15	N	I	S	NA	20.32	71.12	NA	NA	2015-07-22	Adult
LR	13A	N	I	NS	NR	12.7	55.88	10.93	0	2015-07-22	Predation
LR	9	N	I	S	NR	25.4	212.09	6.91	1	2015-07-22	FullyFledgedchick
LR	2	N	I	S	NA	27.94	101.6	16.44	NA	2015-07-22	Adult
LR	17	N	I	S	NR	13.97	63.5	NA	0	2015-07-22	Midfledgedchick
NI	386	A	I	S	R	15.24	76.2	22.22	2	2015-08-07	Fledged
NI	387	A	I	S	R	16.51	81.28	34.87	4	2015-08-07	Fledged
NI	388	A	I	S	NR	11.43	67.31	36.91	4	2015-08-07	Fledged
NI	383	A	I	S	NR	8.89	57.15	27.32	4	2015-08-07	AdultHatchling
NI	384	A	I	S	NR	10.16	57.15	20.84	4	2015-08-07	Eggbroke
NI	1	A	I	S	R	10.16	55.88	33.59	2	2015-08-07	Predation

NI	2	A	I	S	R	17.78	72.39	NA	NA	2015-08-07	EM
NI	284	A	I	S	R	24.13	83.82	19.60	NA	2015-08-07	EM
NI	286	A	I	S	NR	12.7	63.5	20.41	NA	2015-08-07	EM
NI	287	A	I	S	R	22.86	80.01	32.29	0	2015-08-07	DeadMidfledgedchick
NI	300	A	I	S	R	22.86	66.04	32.88	0	2015-08-07	Fledged
NI	391	A	I	S	R	19.05	69.85	11.11	0	2015-08-07	Midfledgedchick
NI	392	A	I	S	NR	15.24	90.17	11.04	0	2015-08-07	Predation
NI	393	A	I	S	R	20.32	71.12	31.40	1	2015-08-07	FullyFledgedchick
NI	3	A	I	S	R	25.4	71.12	52.67	3	2015-08-07	Fledged
NI	4	A	I	S	R	17.78	73.66	51.53	2	2015-08-07	Fledged
NI	5	A	I	S	NR	12.7	48.26	45.50	2	2015-08-07	EM
NI	394	A	I	S	R	15.24	67.31	0.00	0	2015-08-07	Fledged
NI	395	A	I	S	NR	12.7	66.04	0.00	1	2015-08-07	AdultEgg
NI	396	A	I	S	NR	15.24	66.04	0.00	1	2015-08-07	Fledged
NI	397	A	I	S	NR	15.24	71.12	31.45	0	2015-08-07	DeadLatescapchick
NI	288	A	I	S	R	10.16	67.31	3.71	0	2015-08-07	Fledged
NI	289	A	I	S	R	22.86	63.5	NA	NA	2015-08-07	EarlyFledgedchick
NI	398	A	I	S	NR	20.32	68.58	4.95	NA	2015-08-07	EM
NI	299	A	I	S	NR	17.78	67.31	31.45	2	2015-08-07	Fledged
NI	400	A	I	S	NR	17.78	78.74	31.45	NA	2015-08-07	EM
NI	51	N	I	S	NR	16.51	88.9	31.45	2	2015-08-07	Egg2Abandoned
NI	399	A	I	S	NR	17.78	83.82	31.45	3	2015-08-07	Fledged

NI	298	A	I	S	NR	17.78	76.2	31.45	3	2015-08-07	AdultLatescap
NI	6	A	I	S	NR	13.97	64.77	25.23	0	2015-08-07	DeadEarlyscapchick
NI	296	A	I	S	NR	19.05	60.96	31.45	1	2015-08-07	Egg2broke
NI	297	A	I	S	NR	15.24	71.12	31.45	1	2015-08-07	AdultHatchling
NI	7	A	I	S	NR	12.7	64.77	16.21	0	2015-08-07	Adult
NI	8	A	I	S	R	13.97	71.12	29.64	0	2015-08-07	Predation
NI	9	N	I	NS	R	55.88	113.03	13.67	NA	2015-08-07	EM
NI	3A	A	I	S	R	15.24	77.47	16.33	NA	2015-08-07	Adult
NI	376	N	I	S	NR	15.24	121.92	37.87	0	2015-08-07	Fledged
NI	377	N	I	S	R	30.48	127	36.23	0	2015-08-07	Fledged
NI	292	N	I	S	R	31.75	92.71	14.86	0	2015-08-07	Adult
NI	293	N	I	S	R	21.59	77.47	16.16	NA	2015-08-07	EM
NI	378	N	I	S	R	54.61	269.24	36.23	0	2015-08-07	Fledged
NI	CLIFF	N	I	S	NR	19.05	50.8	31.45	NA	2015-08-07	EM
NI	131	A	I	S	NR	15.24	50.8	23.46	1	2015-08-07	Hatchling
NI	132	A	I	S	NR	17.78	62.23	26.00	1	2015-08-07	Midfledgedchick
NI	125	A	I	S	NR	19.05	66.04	7.44	0	2015-08-07	AdultEgg2
NI	133	A	I	S	NR	13.97	60.96	23.28	0	2015-08-07	Fledged
NI	134	A	I	S	NR	13.547	57.15	23.28	1	2015-08-07	AdultHatchling
NI	137	A	I	S	NR	17.78	63.5	23.28	2	2015-08-07	Fledged
NI	135	A	I	S	NR	16.51	57.15	23.28	1	2015-08-07	AdultEgg2
NI	138	A	I	S	R	16.51	50.8	23.28	0	2015-08-07	FullyFledgedchick

NI	139	A	I	NS	R	21.59	68.58	23.28	0	2015-08-07	RatPredation
NI	136	A	I	S	NR	15.24	53.34	28.50	0	2015-08-07	AdultHatchling
NI	127	A	I	S	R	24.13	63.5	28.39	0	2015-08-07	Fledged
NI	128	A	I	S	R	25.4	68.58	19.90	0	2015-08-07	EM
NI	389	A	I	S	NR	17.78	74.93	33.09	1	2015-08-07	Fledged
NI	389A	A	I	S	NR	16.51	69.85	31.98	1	2015-08-07	FullyFledgedchick
NI	389B	N	I	S	R	25.4	63.5	22.88	0	2015-08-07	FullyFledgedchick
PI	1	A	I	S	R	11.43	57.15	NA	1	2015-07-07	Fledged
PI	2	A	I	S	R	10.16	59.69	NA	1	2015-07-07	Fledged
RI	1	A	I	S	NR	19.05	55.88	NA	1	2015-07-25	Halffledgedchick
RI	2	A	I	S	R	22.86	64.77	NA	1	2015-07-25	FullyFledgedchick
RI	3	A	I	S	R	16.51	52.07	NA	0	2015-07-25	EarlyFledgedchick
RIs	1	N	I	S	R	27.94	67.31	NA	NA	2015-07-07	EM
SB	1	A	M	S	R	16.51	67.31	30.00	0	2015-08-28	EM
SB	2	A	M	S	NR	12.7	53.34	26.40	NA	2015-08-28	EM
SB	3	A	M	S	NR	11.43	59.69	26.89	NA	2015-08-28	EM
SB	4	A	M	S	R	11.43	63.5	28.27	0	2015-08-28	EM
SB	15	N	M	S	NR	22.86	83.82	26.12	0	2015-08-28	Fledged
SB	20	N	M	S	NR	60.96	116.84	33.85	0	2015-08-28	RatPredation
SB	19	N	M	S	NR	10.16	109.22	21.89	0	2015-08-28	Halffledgedchick
SB	16	N	M	S	NR	10.16	68.58	19.30	0	2015-08-28	Fledged
SB	21	N	M	S	NR	17.78	86.36	20.89	0	2015-08-28	Fledged

SB	22A	N	M	S	R	12.7	58.42	15.05	0	2015-08-28	Fledged
SB	22	N	M	S	NR	20.32	76.2	32.03	0	2015-08-28	Fledged
SB	23	N	M	S	NR	40.64	132.08	22.45	0	2015-08-28	Fledged
SB	24	N	M	S	NR	10.16	73.66	16.68	NA	2015-08-28	EM
SB	25	N	M	S	NA	22.86	127	20.53	1	2015-08-28	Fledged
SB	25A	N	M	S	NR	15.24	63.5	22.09	1	2015-08-28	Fledged
SB	26	N	M	S	NR	20.32	120.65	35.39	1	2015-08-28	Fledged
SB	27	N	M	S	NR	13.97	72.39	35.94	0	2015-08-28	Eggbroke
SB	28	N	M	S	R	17.78	85.09	35.23	0	2015-08-28	Earlyscapchick
SB	29	N	M	S	NR	16.51	115.57	31.42	0	2015-08-28	Eggbroke
SB	17	N	M	S	R	21.59	78.74	27.71	0	2015-08-28	Fledged
SB	18	N	M	S	NR	12.7	109.22	28.43	0	2015-08-28	EM
SB	30	N	M	NS	NR	15.24	69.85	19.23	NA	2015-08-28	EM
SB	31	N	M	S	NR	11.43	93.98	23.35	0	2015-08-28	Fledged
SB	31A	N	M	NS	NR	22.86	63.5	20.69	NA	2015-08-28	EM
SB	32	A	M	S	NR	10.16	78.74	20.71	0	2015-08-28	Fledged
SI	344	N	I	S	R	25.4	101.6	9.89	NA	2015-08-07	EM
SI	311	N	I	S	R	58.42	87.63	30.33	NA	2015-08-07	EM
SI	361	N	I	S	NR	53.34	143.51	38.50	5	2015-08-07	Fledged
SI	312	N	I	S	NR	30.48	140.97	38.50	NA	2015-08-07	EM
SI	313	N	I	S	R	83.82	96.52	31.83	3	2015-08-07	EggAbandoned
SI	314	N	I	S	NR	39.37	200.66	31.92	NA	2015-08-07	EM

SI	316	N	I	S	NR	33.02	76.2	31.92	5	2015-08-07	Crowpredation
SI	317	N	I	S	NR	10.16	114.3	39.12	5	2015-08-07	Fledged
SI	355	N	I	S	R	12.7	116.84	30.33	1	2015-08-07	Egg2disappeared
SI	320	N	I	S	R	12.7	60.96	39.99	2	2015-08-07	Fledged
SI	341	N	I	S	R	21.59	48.26	30.73	1	2015-08-07	Crowpredation
SI	304	N	I	S	R	16.51	111.76	10.16	0	2015-08-07	Fledged
SI	404	N	I	S	R	55.88	121.92	7.72	0	2015-08-07	Eggbroke
SI	303	N	I	NS	R	35.56	69.85	10.43	NA	2015-08-07	EM
SI	306	N	I	S	R	12.7	72.39	7.37	0	2015-08-07	FullyFledgedchick
SI	307QUA	N	I	S	R	20.32	78.74	10.63	0	2015-08-07	Fledged
SI	366	A	I	S	R	15.24	86.36	49.85	0	2015-08-07	Unknown
SI	367	A	I	S	NR	19.05	83.82	52.04	0	2015-08-07	FullyFledgedchick
SI	368	A	I	S	R	12.7	93.98	52.60	0	2015-08-07	EM
SI	369	A	I	S	NR	15.24	82.55	47.31	1	2015-08-07	Fledged
SI	370	A	I	S	NR	15.24	78.74	41.23	1	2015-08-07	Fledged
SI	371	A	I	S	NR	16.51	96.52	37.89	1	2015-08-07	Fledged
SI	372	A	I	S	NR	16.51	81.28	43.57	1	2015-08-07	Fledged
SP	1	N	M	S	R	20.32	57.15	29.53	1	2015-08-28	Midfledgedchick
SP	1A	N	M	S	R	30.48	162.56	33.80	NA	2015-08-28	EM
SP	2	N	M	S	NR	26.67	236.22	38.56	NA	2015-08-28	EM
SP	3	N	M	S	NR	25.4	236.22	37.87	1	2015-08-28	Fledged
SP	4	N	M	S	NR	20.32	203.2	30.77	1	2015-08-28	Fledged

SP	5	N	M	S	NR	30.48	193.04	46.33	NA	2015-08-28	EM
SP	6	N	M	S	NR	20.32	251.46	55.77	0	2015-08-28	Fledged
SP	7	N	M	S	R	35.56	128	NA	0	2015-08-28	RatPredation
SP	7A	N	M	S	NR	24.13	218.44	36.73	0	2015-08-28	Halffledgedchick
SP	8	N	M	S	NR	22.86	55.88	26.65	0	2015-08-28	Midfledgedchick
SP	9	A	M	S	NR	17.78	90.17	31.81	0	2015-08-28	DeadHatchling
SP	10	N	M	S	R	15.24	152.4	12.83	NA	2015-08-28	EM
SP	11	N	M	S	R	13.97	147	11.43	1	2015-08-28	Fledged
SP	12	N	M	S	NR	17.78	128.27	13.86	1	2015-08-28	RatPredation
SP	13	N	M	NS	NR	40.64	76.2	33.45	NA	2015-08-28	EM
SP	14	N	M	NS	NR	40.64	86.36	18.49	NA	2015-08-28	EM
SP	15	N	M	S	NA	11.43	162.56	32.63	NA	2015-08-28	EM
SP	16	N	M	NS	NR	99.06	105.41	23.28	NA	2015-08-28	EM
SP	17	N	M	NS	NR	31.75	73.66	16.05	NA	2015-08-28	EM
SP	18	N	M	S	NR	16.51	114.3	26.06	0	2015-08-28	Fledged
BA	1	A	M	S	R	12.7	60.96	15.77	NA	2014-08-20	EM
BA	2	A	M	S	R	20.32	85.09	15.72	0	2014-08-20	Fullyfledgedchick
BA	3	A	M	S	NR	12.7	74.93	10.74	0	2014-08-20	Halfhalfchick
BA	4	A	M	S	R	12.7	49.53	23.43	0	2014-08-20	Earlyfledgedchick
BA	5	N	M	S	NR	36.83	67.31	21.04	0	2014-08-20	Earlydownychick
BH	1	A	M	S	R	21.59	109.22	40.03	2	2014-08-20	Hatchling
BH	2	A	M	S	NR	27.94	113.03	40.03	2	2014-08-20	Fullyfledgedchick

BH	3	A	M	S	R	17.78	111.76	40.03	NA	2014-08-20	EM
BH	4	A	M	S	R	20.32	109.855	40.03	0	2014-08-20	Fledged
BH	5	A	M	S	NR	16.51	119.38	40.03	1	2014-08-20	Fledged
BH	6	A	M	S	R	15.24	114.3	40.03	2	2014-08-20	Fledged
BH	7	A	M	S	R	12.7	121.92	40.03	3	2014-08-20	Fullyfledgedchick
BH	8	A	M	S	R	20.32	124.46	40.03	2	2014-08-20	Fledged
BH	9	A	M	S	R	15.24	119.38	40.03	3	2014-08-20	Fledged
BH	10	A	M	S	R	12.7	165.1	40.03	2	2014-08-20	Midfledgedchick
BH	11	A	M	S	R	15.24	139.7	40.03	0	2014-08-20	Fledged
BH	12	A	M	S	R	16.51	152.4	40.03	1	2014-08-20	Fledged
BH	13	A	M	S	R	34.29	139.7	40.03	2	2014-08-20	Fledged
BH	14	A	M	S	NR	33.02	138.43	40.03	1	2014-08-20	Fledged
BH	15	A	M	S	NA	22.86	137.16	40.03	NA	2014-08-20	EM
BH	16	A	M	S	NR	27.94	127	40.03	0	2014-08-20	EM
BH	17	A	M	S	NR	11.43	124.46	40.03	3	2014-08-20	Egg
BH	18	A	M	S	R	22.86	104.14	40.03	2	2014-08-20	Eggfailed
BH	19	A	M	S	NR	16.51	72.39	40.03	0	2014-08-20	EM
BH	20	A	M	S	NR	15.24	71.12	40.03	3	2014-08-20	EM
BH	21	A	M	S	NR	17.78	71.12	40.03	2	2014-08-20	EM
BH	22	A	M	S	NR	16.51	74.93	40.03	NA	2014-08-20	EM
BH	23	A	M	S	NR	15.24	66.04	40.03	NA	2014-08-20	EM
BH	24	A	M	S	R	16.51	64.77	40.03	NA	2014-08-20	EM

BH	25	A	M	S	NR	16.51	69.85	40.03	NA	2014-08-20	EM
BH	26	A	M	S	NR	17.78	71.12	40.03	NA	2014-08-20	EM
BH	27	A	M	S	NR	16.51	67.31	40.03	NA	2014-08-20	EM
BH	28	A	M	S	NR	15.24	64.77	40.03	NA	2014-08-20	EM
BH	29	A	M	S	NR	15.24	79.24	40.03	NA	2014-08-20	EM
BH	30	A	M	S	R	17.78	67.31	40.03	NA	2014-08-20	EM
BH	31	A	M	S	R	20.32	64.77	40.03	NA	2014-08-20	EM
BH	32	A	M	S	NR	20.32	64.77	40.03	NA	2014-08-20	EM
BH	33	A	M	S	NR	19.05	77.47	40.03	NA	2014-08-20	EM
BH	34	A	M	S	NR	17.78	63.5	40.03	NA	2014-08-20	EM
BH	35	A	M	S	NR	17.78	71.12	40.03	NA	2014-08-20	EM
BH	36	A	M	S	NR	16.51	68.58	40.03	NA	2014-08-20	EM
BH	37	A	M	S	NR	16.51	66.04	40.03	NA	2014-08-20	EM
BH	38	A	M	S	R	13.97	68.58	40.03	NA	2014-08-20	EM
BH	39	A	M	S	R	17.78	72.39	40.03	NA	2014-08-20	EM
BH	40	A	M	S	NR	27.94	73.66	40.03	NA	2014-08-20	EM
BH	41	A	M	S	NR	15.875	77.47	40.03	NA	2014-08-20	EM
BH	42	A	M	S	NR	16.51	80.01	40.03	NA	2014-08-20	EM
BH	43	A	M	S	NR	16.51	62.23	40.03	2	2014-08-20	Egg
CI	1	A	I	S	NR	11.43	73.66	NA	NA	2014-07-07	Adult
CI	2	A	I	S	R	15.24	55.88	NA	1	2014-07-07	DeadEarlydownychick
CIs	1	A	M	S	NR	22.86	76.2	17.97	1	2014-08-22	Latescapchick

CIs	2	A	M	S	NR	15.24	63.5	31.97	1	2014-08-22	Fledged
CIs	3	A	M	NS	R	13.97	53.34	48.69	0	2014-08-22	Fullyfledgedchick
CIs	4	A	M	S	NR	15.24	63.5	30.56	0	2014-08-22	Deaddownychick
CIs	4A	A	M	S	NR	16.51	66.04	12.95	NA	2014-08-22	EM
CIs	4B	A	M	S	R	13.97	66.04	36.14	0	2014-08-22	Fledged
CIs	4C	A	M	S	R	20.32	60.96	30.04	NA	2014-08-22	EM
CIs	4D	A	M	S	R	16.51	69.85	22.02	NA	2014-08-22	EM
CIs	5	A	M	S	R	20.32	66.04	0.00	NA	2014-08-22	EM
CIs	6	A	M	S	R	12.7	60.96	26.41	NA	2014-08-22	EM
CIs	7	A	M	S	R	12.7	63.5	28.83	NA	2014-08-22	EM
CIs	8	A	M	S	R	15.24	55.88	1.00	NA	2014-08-22	EM
CIs	9	A	M	S	NR	17.78	63.5	0.24	NA	2014-08-22	EM
CIs	10	A	M	S	R	15.24	63.5	0.13	0	2014-08-22	Fledged
CIs	11	A	M	S	R	17.78	62.23	17.54	NA	2014-08-22	EM
CIs	12	A	M	S	R	12.7	63.5	35.69	NA	2014-08-22	EM
CIs	13	N	M	S	R	25.4	71.12	47.67	NA	2014-08-22	EM
CIs	14	A	M	S	R	15.24	66.04	35.29	NA	2014-08-22	EM
CIs	15	A	M	S	R	20.32	62.23	32.37	NA	2014-08-22	EM
CIs	16	A	M	S	R	17.78	60.96	44.17	NA	2014-08-22	EM
CIs	17	A	M	S	R	12.7	63.5	35.33	NA	2014-08-22	EM
CIs	18	A	M	S	NR	16.51	59.69	22.15	NA	2014-08-22	EM
CIs	19	N	M	S	NR	16.51	96.52	37.48	NA	2014-08-22	EM

CIs	20	A	M	S	R	15.24	76.2	14.99	NA	2014-08-22	EM
CIs	21	A	M	S	R	12.7	66.04	31.30	NA	2014-08-22	EM
CIs	22	A	M	S	NR	15.24	63.5	38.62	NA	2014-08-22	EM
CIs	23	A	M	S	R	16.51	60.96	27.58	0	2014-08-22	Eggbroke
CIs	24	A	M	S	R	15.24	57.15	11.54	NA	2014-08-22	EM
CIs	25	A	M	S	R	15.24	54.61	30.01	NA	2014-08-22	EM
CIs	26	A	M	S	R	15.24	67.31	32.77	NA	2014-08-22	EM
CIs	27	A	M	S	R	15.24	66.04	24.10	NA	2014-08-22	EM
CIs	28	A	M	S	R	12.7	55.88	29.22	0	2014-08-22	Egg
DH	1	A	M	S	R	13.97	104.14	30.98	0	2014-08-21	Fledged
DH	2	A	M	S	NA	16.51	104.14	30.98	NA	2014-08-21	Unknown
DH	3	A	M	S	NA	15.24	114.3	30.98	0	2014-08-21	Fledged
DH	4	A	M	S	NA	16.51	129.54	29.93	0	2014-08-21	Fledged
DH	5	A	M	S	NA	17.78	134.62	41.68	NA	2014-08-21	EM
DH	6	A	M	S	NA	20.532	129.54	42.08	0	2014-08-21	Fledged
DH	7	A	M	S	NA	12.7	111.76	34.46	NA	2014-08-21	EM
DH	8	A	M	S	NR	12.7	111.76	34.70	0	2014-08-21	Midfledgedchick
DH	9	A	M	S	R	13.97	107.95	34.70	0	2014-08-21	Earlyfledgedchick
DH	10	A	M	S	NR	15.24	110.49	34.70	NA	2014-08-21	Adult
DH	11	A	M	S	NR	12.7	96.52	34.70	0	2014-08-21	Fledged
DH	12	A	M	S	NR	15.24	105.41	15.29	0	2014-08-21	Fledged
DH	13	A	M	S	R	16.51	93.98	28.46	0	2014-08-21	Midfledgedchick

DH	1	N	M	S	NR	38.1	69.85	29.06	NA	2014-08-21	EM
DH	2	N	M	S	NR	16.51	113.03	24.60	0	2014-08-21	Halfhalfchick
FR	1	N	M	S	NR	17.78	259.08	36.61	NA	2014-08-22	EM
FR	2	N	M	S	NR	30.48	55.88	36.70	NA	2014-08-22	EM
FR	3	N	M	S	NA	40.64	104.14	44.37	1	2014-08-22	Fledged
FR	4	N	M	S	NA	30.48	182.88	45.66	1	2014-08-22	Unknown
FR	5	N	M	S	NA	24.765	164.465	27.03	NA	2014-08-22	EM
FR	6	N	M	NS	NR	63.5	60.96	11.79	NA	2014-08-22	EM
FR	6A	N	M	S	NR	40.64	97.79	24.59	0	2014-08-22	Fledged
FR	6B	N	M	S	NR	35.56	30.48	19.28	0	2014-08-22	Fledged
FR	6C	N	M	S	NR	22.225	54.61	13.01	NA	2014-08-22	EM
FR	6D	N	M	NS	R	25.4	54.61	18.72	NA	2014-08-22	EM
FR	6E	N	M	S	R	26.67	100.33	19.02	NA	2014-08-22	EM
FR	6F	N	M	S	R	27.94	74.93	20.76	NA	2014-08-22	EM
FR	7	N	M	S	R	12.7	81.28	26.47	0	2014-08-22	Fullyfledgedchick
FR	7A	N	M	NS	R	31.75	129.54	34.41	NA	2014-08-22	EM
FR	7A1	N	M	NS	R	27.94	127	27.42	0	2014-08-22	Eggbroke
FR	7B	N	M	NS	NR	25.4	76.2	20.50	NA	2014-08-22	EM
FR	8	N	M	S	NR	15.24	86.36	23.60	0	2014-08-22	Fledged
FR	8A	N	M	NS	NR	33.02	58.42	24.38	NA	2014-08-22	EM
FR	9	N	M	S	R	31.75	74.93	20.89	NA	2014-08-22	EM
FR	10	N	M	S	R	12.7	83.82	49.00	2	2014-08-22	Fledged

FR	10A	N	M	S	R	16.51	63.5	48.47	2	2014-08-22	Fledged
FR	10B	N	M	S	NA	17.78	128.27	48.47	2	2014-08-22	Unknown
FR	11	N	M	S	NR	19.05	91.44	22.90	0	2014-08-22	Fledged
FR	11A	N	M	S	NR	25.4	63.5	30.64	NA	2014-08-22	EM
FR	11B	N	M	S	NR	30.48	101.6	15.63	NA	2014-08-22	EM
FR	11C	N	M	S	NR	17.78	52.07	13.65	NA	2014-08-22	EM
FR	12	N	M	S	NR	25.4	68.58	9.52	NA	2014-08-22	EM
FR	13	N	M	S	NR	20.32	123.19	12.48	0	2014-08-22	Eggdisappeared
FR	13A	N	M	S	R	27.94	72.39	13.79	NA	2014-08-22	EM
FR	14	N	M	NS	NR	21.59	71.12	43.15	NA	2014-08-22	EM
FR	14A	N	M	NS	NR	15.24	53.34	32.96	NA	2014-08-22	EM
FR	15	N	M	S	NR	22.86	58.42	14.87	NA	2014-08-22	EM
FR	16	N	M	S	NR	48.26	78.74	18.56	NA	2014-08-22	EM
FR	16A	N	M	S	NR	45.72	87.63	17.33	NA	2014-08-22	EM
FR	16B	N	M	S	NR	17.78	38.1	20.28	NA	2014-08-22	EM
FR	17	N	M	S	R	45.72	91.44	35.40	0	2014-08-22	Eggbroke
FR	18	N	M	S	R	10.16	55.88	27.71	3	2014-08-22	Midscapchick
FR	19	N	M	S	NR	29.21	91.44	27.71	NA	2014-08-22	EM
FR	20	N	M	S	R	39.37	127	27.71	2	2014-08-22	Midscapchick
FR	21	N	M	S	R	29.21	50.8	27.15	2	2014-08-22	Fledged
FR	22	N	M	S	NR	27.94	86.36	34.33	1	2014-08-22	Earlyfledgedchick
FR	22A	N	M	S	NR	19.05	71.12	15.83	NA	2014-08-22	EM

FR	23	N	M	S	R	22.86	66.04	13.52	NA	2014-08-22	EM
FR	24	N	M	S	R	22.86	60.96	14.30	NA	2014-08-22	EM
FR	24A	N	M	S	NA	41.91	114.3	23.07	NA	2014-08-22	EM
FR	24B	N	M	S	NR	22.86	181.61	31.91	0	2014-08-22	Adult
FR	24C	N	M	S	R	34.29	76.2	15.08	0	2014-08-22	Fledged
FR	24D	N	M	S	R	17.78	71.12	23.93	0	2014-08-22	Fullyfledgedchick
FR	24E	N	M	S	NR	17.78	60.96	5.68	0	2014-08-22	Eggbroke
FR	25	N	M	S	R	27.94	113.03	39.05	0	2014-08-22	DeadEarlydownychick
GI	1	A	I	S	NR	25.4	76.2	NA	2	2014-08-01	Fullyfledgechick
GI	2	A	I	S	R	20.32	76.2	NA	2	2014-08-01	Fledged
GI	3	A	I	S	R	15.24	67.31	NA	2	2014-08-01	Fledged
GI	4	A	I	S	NR	19.05	67.31	NA	0	2014-08-01	AdultFullyfledgechick
GI	5	N	I	S	NR	19.05	40.64	27.70	0	2014-08-01	Fledged
HR	265	N	I	S	R	30.48	58.42	38.60	NA	2014-08-15	EM
HR	263	N	I	S	R	17.78	55.88	39.92	NA	2014-08-15	EM
HR	262	A	I	S	NR	12.7	78.74	39.92	1	2014-08-15	Fullyfledgedchick
HR	205	N	I	S	NR	25.4	69.85	29.49	1	2014-08-15	EM
HR	1	N	I	S	R	20.32	48.26	37.40	NA	2014-08-15	EM
HR	268	N	I	S	NR	22.86	59.69	24.57	0	2014-08-15	Halfhalfchick
HR	269A	N	I	S	R	38.1	114.3	24.20	NA	2014-08-15	EM
HR	269	A	I	S	R	27.94	133.35	28.19	NA	2014-08-15	EM
HR	270	A	I	S	NR	17.78	68.58	28.77	0	2014-08-15	Halfhalfchick

HR	271	A	I	S	R	21.59	71.12	24.84	0	2014-08-15	Halfhalfchick
HR	273	A	I	S	NR	13.97	66.04	22.35	1	2014-08-15	Fullyfledgedchick
HR	274	A	I	S	R	10.16	59.69	27.59	1	2014-08-15	Fullyfledgedchick
HR	283	A	I	S	NR	11.43	63.5	29.53	NA	2014-08-15	EM
HR	282	A	I	S	NR	10.16	63.5	21.84	NA	2014-08-15	Adult
HR	279	N	I	S	R	27.94	60.96	19.82	NA	2014-08-15	EM
HR	1A	N	I	S	R	33.02	78.74	24.04	NA	2014-08-15	EM
HR	1B	N	I	S	NR	20.32	40.64	25.48	0	2014-08-15	Fullyfledgedchick
LI	1	A	I	S	R	10.16	55.88	NA	0	2014-08-01	Fledged
LI	2	A	I	S	R	10.16	71.12	NA	NA	2014-08-01	EM
LI	3	A	I	S	NR	7.62	58.42	NA	0	2014-08-01	AdultEarlydownychick
NI	386	A	I	S	R	15.24	76.2	22.22	NA	2014-08-20	EM
NI	387	A	I	S	R	16.51	81.28	34.87	0	2014-08-20	Fledged
NI	388	A	I	S	NR	11.43	67.31	36.91	NA	2014-08-20	EM
NI	383	A	I	S	NR	8.89	57.15	27.32	NA	2014-08-20	EM
NI	384	A	I	S	NR	10.16	57.15	20.84	NA	2014-08-20	EM
NI	1	A	I	S	R	10.16	55.88	33.59	0	2014-08-20	Fledged
NI	2	A	I	S	R	17.78	72.39	NA	NA	2014-08-20	EM
NI	284	A	I	S	R	24.13	83.82	19.60	NA	2014-08-20	EM
NI	286	A	I	S	NR	12.7	63.5	20.41	NA	2014-08-20	EM
NI	287	A	I	S	R	22.86	80.01	32.29	0	2014-08-20	Middownychick
NI	300	A	I	S	R	22.86	66.04	32.88	0	2014-08-20	Eggbroke

NI	391	A	I	S	R	19.05	69.85	11.11	0	2014-08-20	Fledged
NI	392	A	I	S	NR	15.24	90.17	11.04	0	2014-08-20	Midfledgedchick
NI	393	A	I	S	R	20.32	71.12	31.40	1	2014-08-20	Unknown
NI	3	A	I	S	R	25.4	71.12	52.67	3	2014-08-20	Midfledgedchick
NI	4	A	I	S	R	17.78	73.66	51.53	2	2014-08-20	Fledged
NI	5	A	I	S	NR	12.7	48.26	45.50	2	2014-08-20	Fledged
NI	394	A	I	S	R	15.24	67.31	0.00	0	2014-08-20	Unknown
NI	395	A	I	S	NR	12.7	66.04	0.00	1	2014-08-20	CrowPredation
NI	396	A	I	S	NR	15.24	66.04	0.00	1	2014-08-20	Fledged
NI	397	A	I	S	NR	15.24	71.12	31.45	0	2014-08-20	Earlyscapchick
NI	288	A	I	S	R	10.16	67.31	3.71	0	2014-08-20	Eggbroke
NI	289	A	I	S	R	22.86	63.5	NA	NA	2014-08-20	Fledged
NI	398	A	I	S	NR	20.32	68.58	4.95	0	2014-08-20	Fullyfledgedchick
NI	299	A	I	S	NR	17.78	67.31	31.45	NA	2014-08-20	EM
NI	400	A	I	S	NR	17.78	78.74	31.45	3	2014-08-20	Fledged
NI	51	N	I	S	NR	16.51	88.9	31.45	3	2014-08-20	EM
NI	399	A	I	S	NR	17.78	83.82	31.45	3	2014-08-20	Fledged
NI	298	A	I	S	NR	17.78	76.2	31.45	3	2014-08-20	Fledged
NI	6	A	I	S	NR	13.97	64.77	25.23	NA	2014-08-20	EM
NI	296	A	I	S	NR	19.05	60.96	31.45	1	2014-08-20	Fledged
NI	297	A	I	S	NR	15.24	71.12	31.45	1	2014-08-20	Fledged
NI	7	A	I	S	NR	12.7	64.77	16.21	0	2014-08-20	Fullyfledgedchick

NI	8	A	I	S	R	13.97	71.12	29.64	NA	2014-08-20	EM
NI	9	N	I	NS	R	55.88	113.03	13.67	NA	2014-08-20	EM
NI	3A	A	I	S	R	15.24	77.47	16.33	NA	2014-08-20	Adult
NI	376	N	I	S	NR	15.24	121.92	37.87	0	2014-08-20	Fledged
NI	377	N	I	S	R	30.48	127	36.23	1	2014-08-20	Fullyfledgedchick
NI	292	N	I	S	R	31.75	92.71	14.86	NA	2014-08-20	EM
NI	293	N	I	S	R	21.59	77.47	16.16	NA	2014-08-20	Adult
NI	378	N	I	S	R	54.61	269.24	36.23	NA	2014-08-20	EM
NI	CLIFF	N	I	S	NR	19.05	50.8	31.45	1	2014-08-20	Fledged
NI	131	A	I	S	NR	15.24	50.8	23.46	0	2014-08-20	EM
NI	132	A	I	S	NR	17.78	62.23	26.00	NA	2014-08-20	EM
NI	125	A	I	S	NR	19.05	66.04	7.44	0	2014-08-20	Fledged
NI	133	A	I	S	NR	13.97	60.96	23.28	0	2014-08-20	Midscapchick
NI	134	A	I	S	NR	13.547	57.15	23.28	1	2014-08-20	EM
NI	137	A	I	S	NR	17.78	63.5	23.28	1	2014-08-20	Eggfailed
NI	135	A	I	S	NR	16.51	57.15	23.28	NA	2014-08-20	EM
NI	138	A	I	S	R	16.51	50.8	23.28	0	2014-08-20	Eggbroke
NI	139	A	I	NS	R	21.59	68.58	23.28	0	2014-08-20	EM
NI	136	A	I	S	NR	15.24	53.34	28.50	0	2014-08-20	Predation
NI	127	A	I	S	R	24.13	63.5	28.39	0	2014-08-20	Fledged
NI	128	A	I	S	R	25.4	68.58	19.90	0	2014-08-20	EM
NI	389	A	I	S	NR	17.78	74.93	33.09	1	2014-08-20	Fledged

NI	389A	A	I	S	NR	16.51	69.85	31.98	1	2014-08-20	Latedownychick
NI	389B	N	I	S	R	25.4	63.5	22.88	0	2014-08-20	Fullyfledgedchick
PI	1	A	I	S	R	11.43	57.15	NA	1	2014-08-01	Fledged
PI	2	A	I	S	R	10.16	59.69	NA	1	2014-08-01	Fledged
RI	1	A	I	S	NR	19.05	55.88	NA	1	2014-08-01	Fledged
RI	2	A	I	S	R	22.86	64.77	NA	1	2014-08-01	Fledged
RI	3	A	I	S	R	16.51	52.07	NA	NA	2014-08-01	Adult
RIs	1	N	I	S	R	27.94	67.31	NA	NA	2014-08-01	EM
SB	1	A	M	S	R	16.51	67.31	30.00	0	2014-08-09	Eggbroke
SB	2	A	M	S	NR	12.7	53.34	26.40	NA	2014-08-09	EM
SB	3	A	M	S	NR	11.43	59.69	26.89	NA	2014-08-09	EM
SB	4	A	M	S	R	11.43	63.5	28.27	0	2014-08-09	Eggbroke
SB	15	N	M	S	NR	22.86	83.82	26.12	0	2014-08-09	AdultEarlydownychick
SB	20	N	M	S	NR	60.96	116.84	33.85	0	2014-08-09	Latedownychick
SB	19	N	M	S	NR	10.16	109.22	21.89	NA	2014-08-09	EM
SB	16	N	M	S	NR	10.16	68.58	19.30	0	2014-08-09	Fledged
SB	21	N	M	S	NR	17.78	86.36	20.89	NA	2014-08-09	EM
SB	22A	N	M	S	R	12.7	58.42	15.05	0	2014-08-09	Fledged
SB	22	N	M	S	NR	20.32	76.2	32.03	0	2014-08-09	Earlyfledgechick
SB	23	N	M	S	NR	40.64	132.08	22.45	0	2014-08-09	Fledged
SB	24	N	M	S	NR	10.16	73.66	16.68	0	2014-08-09	Fledged
SB	25	N	M	S	NA	22.86	127	20.53	1	2014-08-09	Fledged

SB	25A	N	M	S	NR	15.24	63.5	22.09	1	2014-08-09	Fledged
SB	26	N	M	S	NR	20.32	120.65	35.39	0	2014-08-09	Fledged
SB	27	N	M	S	NR	13.97	72.39	35.94	NA	2014-08-09	EM
SB	28	N	M	S	R	17.78	85.09	35.23	NA	2014-08-09	EM
SB	29	N	M	S	NR	16.51	115.57	31.42	NA	2014-08-09	EM
SB	17	N	M	S	R	21.59	78.74	27.71	0	2014-08-09	Fledged
SB	18	N	M	S	NR	12.7	109.22	28.43	0	2014-08-09	Fledged
SB	30	N	M	NS	NR	15.24	69.85	19.23	NA	2014-08-09	EM
SB	31	N	M	S	NR	11.43	93.98	23.35	NA	2014-08-09	EM
SB	31A	N	M	NS	NR	22.86	63.5	20.69	NA	2014-08-09	EM
SB	32	A	M	S	NR	10.16	78.74	20.71	0	2014-08-09	Latefledgechick
SI	344	N	I	S	R	25.4	101.6	9.89	NA	2014-08-15	EM
SI	311	N	I	S	R	58.42	87.63	30.33	NA	2014-08-15	EM
SI	361	N	I	S	NR	53.34	143.51	38.50	4	2014-08-15	Fledged
SI	312	N	I	S	NR	30.48	140.97	38.50	3	2014-08-15	Fledged
SI	313	N	I	S	R	83.82	96.52	31.83	NA	2014-08-15	EM
SI	314	N	I	S	NR	39.37	200.66	31.92	NA	2014-08-15	Adult
SI	316	N	I	S	NR	33.02	76.2	31.92	NA	2014-08-15	EM
SI	317	N	I	S	NR	10.16	114.3	39.12	4	2014-08-15	Fledged
SI	355	N	I	S	R	12.7	116.84	30.33	1	2014-08-15	Eggbroke
SI	320	N	I	S	R	12.7	60.96	39.99	1	2014-08-15	Fledged
SI	341	N	I	S	R	21.59	48.26	30.73	NA	2014-08-15	EM

SI	304	N	I	S	R	16.51	111.76	10.16	NA	2014-08-15	EM
SI	404	N	I	S	R	55.88	121.92	7.72	0	2014-08-15	Eggbroke
SI	303	N	I	NS	R	35.56	69.85	10.43	NA	2014-08-15	EM
SI	306	N	I	S	R	12.7	72.39	7.37	NA	2014-08-15	EM
SI	307QUA	N	I	S	R	20.32	78.74	10.63	0	2014-08-15	Fledged
SI	366	A	I	S	R	15.24	86.36	49.85	NA	2014-08-15	EM
SI	367	A	I	S	NR	19.05	83.82	52.04	0	2014-08-15	AdultEarlydownychick
SI	368	A	I	S	R	12.7	93.98	52.60	0	2014-08-15	Halfhalfchick
SI	369	A	I	S	NR	15.24	82.55	47.31	1	2014-08-15	Fledged
SI	370	A	I	S	NR	15.24	78.74	41.23	1	2014-08-15	Fledged
SI	371	A	I	S	NR	16.51	96.52	37.89	NA	2014-08-15	EM
SI	372	A	I	S	NR	16.51	81.28	43.57	0	2014-08-15	Fullyfledgedchick
SP	1	N	M	S	R	20.32	57.15	29.53	0	2014-08-21	Middownychick
SP	1A	N	M	S	R	30.48	162.56	33.80	NA	2014-08-21	EM
SP	2	N	M	S	NR	26.67	236.22	38.56	NA	2014-08-21	EM
SP	3	N	M	S	NR	25.4	236.22	37.87	1	2014-08-21	Fledged
SP	4	N	M	S	NR	20.32	203.2	30.77	1	2014-08-21	Fledged
SP	5	N	M	S	NR	30.48	193.04	46.33	NA	2014-08-21	EM
SP	6	N	M	S	NR	20.32	251.46	55.77	0	2014-08-21	Fledged
SP	7	N	M	S	R	35.56	128	NA	0	2014-08-21	Fledged
SP	7A	N	M	S	NR	24.13	218.44	36.73	0	2014-08-21	Fledged
SP	8	N	M	S	NR	22.86	55.88	26.65	0	2014-08-21	AdultEarlydownychick

SP	9	A	M	S	NR	17.78	90.17	31.81	0	2014-08-21	Midfledgedchick
SP	10	N	M	S	R	15.24	152.4	12.83	NA	2014-08-21	EM
SP	11	N	M	S	R	13.97	147	11.43	1	2014-08-21	Fledged
SP	12	N	M	S	NR	17.78	128.27	13.86	1	2014-08-21	Midfledgedchick
SP	13	N	M	NS	NR	40.64	76.2	33.45	NA	2014-08-21	EM
SP	14	N	M	NS	NR	40.64	86.36	18.49	NA	2014-08-21	EM
SP	15	N	M	S	NA	11.43	162.56	32.63	NA	2014-08-21	EM
SP	16	N	M	NS	NR	99.06	105.41	23.28	NA	2014-08-21	EM
SP	17	N	M	NS	NR	31.75	73.66	16.05	NA	2014-08-21	EM
SP	18	N	M	S	NR	16.51	114.3	26.06	0	2014-08-21	RatPredation
BA	1	A	M	S	R	12.7	60.96	15.77	NA	2013-08-20	EM
BA	2	A	M	S	R	20.32	85.09	15.72	0	2013-08-20	Fledged
BA	3	A	M	S	NR	12.7	74.93	10.74	0	2013-08-20	Chick
BA	4	A	M	S	R	12.7	49.53	23.43	NA	2013-08-20	EM
BA	5	N	M	S	NR	36.83	67.31	21.04	0	2013-08-20	Chick
BH	1	A	M	S	R	21.59	109.22	40.03	NA	2013-08-12	EM
BH	2	A	M	S	NR	27.94	113.03	40.03	NA	2013-08-12	EM
BH	3	A	M	S	R	17.78	111.76	40.03	NA	2013-08-12	EM
BH	4	A	M	S	R	20.32	109.855	40.03	NA	2013-08-12	EM
BH	5	A	M	S	NR	16.51	119.38	40.03	1	2013-08-12	Fledged
BH	6	A	M	S	R	15.24	114.3	40.03	1	2013-08-12	Chick
BH	7	A	M	S	R	12.7	121.92	40.03	NA	2013-08-12	EM

BH	8	A	M	S	R	20.32	124.46	40.03	1	2013-08-12	Chick
BH	9	A	M	S	R	15.24	119.38	40.03	2	2013-08-12	Chick
BH	10	A	M	S	R	12.7	165.1	40.03	2	2013-08-12	Chick
BH	11	A	M	S	R	15.24	139.7	40.03	1	2013-08-12	Fledged
BH	12	A	M	S	R	16.51	152.4	40.03	NA	2013-08-12	EM
BH	13	A	M	S	R	34.29	139.7	40.03	1	2013-08-12	Fledged
BH	14	A	M	S	NR	33.02	138.43	40.03	1	2013-08-12	Chick
BH	15	A	M	S	NA	22.86	137.16	40.03	1	2013-08-12	Chick
BH	16	A	M	S	NR	27.94	127	40.03	1	2013-08-12	Fledged
BH	17	A	M	S	NR	11.43	124.46	40.03	2	2013-08-12	Fledged
BH	18	A	M	S	R	22.86	104.14	40.03	2	2013-08-12	Chick
BH	19	A	M	S	NR	16.51	72.39	40.03	2	2013-08-12	Egg
BH	20	A	M	S	NR	15.24	71.12	40.03	NA	2013-08-12	EM
BH	21	A	M	S	NR	17.78	71.12	40.03	1	2013-08-12	EM
BH	22	A	M	S	NR	16.51	74.93	40.03	NA	2013-08-12	EM
BH	23	A	M	S	NR	15.24	66.04	40.03	NA	2013-08-12	EM
BH	24	A	M	S	R	16.51	64.77	40.03	NA	2013-08-12	EM
BH	25	A	M	S	NR	16.51	69.85	40.03	NA	2013-08-12	EM
BH	26	A	M	S	NR	17.78	71.12	40.03	NA	2013-08-12	EM
BH	27	A	M	S	NR	16.51	67.31	40.03	NA	2013-08-12	EM
BH	28	A	M	S	NR	15.24	64.77	40.03	NA	2013-08-12	EM
BH	29	A	M	S	NR	15.24	79.24	40.03	NA	2013-08-12	EM

BH	30	A	M	S	R	17.78	67.31	40.03	NA	2013-08-12	EM
BH	31	A	M	S	R	20.32	64.77	40.03	NA	2013-08-12	EM
BH	32	A	M	S	NR	20.32	64.77	40.03	NA	2013-08-12	EM
BH	33	A	M	S	NR	19.05	77.47	40.03	NA	2013-08-12	EM
BH	34	A	M	S	NR	17.78	63.5	40.03	NA	2013-08-12	EM
BH	35	A	M	S	NR	17.78	71.12	40.03	NA	2013-08-12	EM
BH	36	A	M	S	NR	16.51	68.58	40.03	NA	2013-08-12	EM
BH	37	A	M	S	NR	16.51	66.04	40.03	NA	2013-08-12	EM
BH	38	A	M	S	R	13.97	68.58	40.03	NA	2013-08-12	EM
BH	39	A	M	S	R	17.78	72.39	40.03	NA	2013-08-12	EM
BH	40	A	M	S	NR	27.94	73.66	40.03	NA	2013-08-12	EM
BH	41	A	M	S	NR	15.875	77.47	40.03	NA	2013-08-12	EM
BH	42	A	M	S	NR	16.51	80.01	40.03	NA	2013-08-12	EM
BH	43	A	M	S	NR	16.51	62.23	40.03	NA	2013-08-12	EM
BI	1	N	I	S	NA	20.32	64.77	14.62	0	2013-08-16	Fledged
BI	2	N	I	S	NA	31.75	132.08	NA	NA	2013-08-16	Fledged
BI	3	N	I	S	NA	25.4	80.01	NA	NA	2013-08-16	Chick
BI	4	N	I	S	NA	22.86	127	NA	0	2013-08-16	Fledged
BI	5	N	I	S	NA	25.4	80.01	NA	NA	2013-08-16	EM
BI	6	N	I	S	NA	7.62	44.45	NA	NA	2013-08-16	Chick
BI	7	N	I	S	NA	20.32	101.6	NA	NA	2013-08-16	Chick
BI	7A	N	I	S	NA	29.21	81.28	NA	NA	2013-08-16	Chick

BI	8	N	I	S	NA	15.24	59.69	NA	NA	2013-08-16	Chick
BI	9	N	I	S	NA	38.1	81.28	NA	NA	2013-08-16	EM
BI	10	N	I	S	NA	30.48	77.47	NA	NA	2013-08-16	Chick
BI	18	N	I	S	NA	25.4	85.09	NA	NA	2013-08-16	EM
CI	1	A	I	S	NR	11.43	73.66	NA	1	2013-08-16	Fledged
CI	2	A	I	S	R	15.24	55.88	NA	1	2013-08-16	EM
CIs	1	A	M	S	NR	22.86	76.2	17.97	NA	2013-08-21	EM
CIs	2	A	M	S	NR	15.24	63.5	31.97	0	2013-08-21	Chick
CIs	3	A	M	NS	R	13.97	53.34	48.69	NA	2013-08-21	EM
CIs	4	A	M	S	NR	15.24	63.5	30.56	0	2013-08-21	Chick
CIs	4A	A	M	S	NR	16.51	66.04	12.95	NA	2013-08-21	EM
CIs	4B	A	M	S	R	13.97	66.04	36.14	0	2013-08-21	Chick
CIs	4C	A	M	S	R	20.32	60.96	30.04	NA	2013-08-21	EM
CIs	4D	A	M	S	R	16.51	69.85	22.02	NA	2013-08-21	EM
CIs	5	A	M	S	R	20.32	66.04	0.00	NA	2013-08-21	EM
CIs	6	A	M	S	R	12.7	60.96	26.41	NA	2013-08-21	EM
CIs	7	A	M	S	R	12.7	63.5	28.83	NA	2013-08-21	EM
CIs	8	A	M	S	R	15.24	55.88	1.00	NA	2013-08-21	EM
CIs	9	A	M	S	NR	17.78	63.5	0.24	NA	2013-08-21	EM
CIs	10	A	M	S	R	15.24	63.5	0.13	NA	2013-08-21	EM
CIs	11	A	M	S	R	17.78	62.23	17.54	NA	2013-08-21	EM
CIs	12	A	M	S	R	12.7	63.5	35.69	NA	2013-08-21	EM

CIs	13	N	M	S	R	25.4	71.12	47.67	NA	2013-08-21	EM
CIs	14	A	M	S	R	15.24	66.04	35.29	NA	2013-08-21	EM
CIs	15	A	M	S	R	20.32	62.23	32.37	NA	2013-08-21	EM
CIs	16	A	M	S	R	17.78	60.96	44.17	NA	2013-08-21	EM
CIs	17	A	M	S	R	12.7	63.5	35.33	NA	2013-08-21	EM
CIs	18	A	M	S	NR	16.51	59.69	22.15	NA	2013-08-21	EM
CIs	19	N	M	S	NR	16.51	96.52	37.48	NA	2013-08-21	EM
CIs	20	A	M	S	R	15.24	76.2	14.99	NA	2013-08-21	EM
CIs	21	A	M	S	R	12.7	66.04	31.30	NA	2013-08-21	EM
CIs	22	A	M	S	NR	15.24	63.5	38.62	NA	2013-08-21	EM
CIs	23	A	M	S	R	16.51	60.96	27.58	NA	2013-08-21	EM
CIs	24	A	M	S	R	15.24	57.15	11.54	NA	2013-08-21	EM
CIs	25	A	M	S	R	15.24	54.61	30.01	NA	2013-08-21	EM
CIs	26	A	M	S	R	15.24	67.31	32.77	NA	2013-08-21	EM
CIs	27	A	M	S	R	15.24	66.04	24.10	NA	2013-08-21	EM
CIs	28	A	M	S	R	12.7	55.88	29.22	NA	2013-08-21	EM
DH	1	A	M	S	R	13.97	104.14	30.98	0	2013-08-08	Chick
DH	2	A	M	S	NA	16.51	104.14	30.98	NA	2013-08-08	EM
DH	3	A	M	S	NA	15.24	114.3	30.98	NA	2013-08-08	EM
DH	4	A	M	S	NA	16.51	129.54	29.93	NA	2013-08-08	EM
DH	5	A	M	S	NA	17.78	134.62	41.68	0	2013-08-08	Chick
DH	6	A	M	S	NA	20.532	129.54	42.08	1	2013-08-08	Chick

DH	7	A	M	S	NA	12.7	111.76	34.46	1	2013-08-08	Chick
DH	8	A	M	S	NR	12.7	111.76	34.70	0	2013-08-08	Chick
DH	9	A	M	S	R	13.97	107.95	34.70	0	2013-08-08	Chick
DH	10	A	M	S	NR	15.24	110.49	34.70	0	2013-08-08	Chick
DH	11	A	M	S	NR	12.7	96.52	34.70	0	2013-08-08	Chick
DH	12	A	M	S	NR	15.24	105.41	15.29	0	2013-08-08	Chick
DH	13	A	M	S	R	16.51	93.98	28.46	NA	2013-08-08	EM
DH	1	N	M	S	NR	38.1	69.85	29.06	0	2013-08-08	Chick
DH	2	N	M	S	NR	16.51	113.03	24.60	0	2013-08-08	Chick
FR	1	N	M	S	NR	17.78	259.08	36.61	0	2013-08-10	Chick
FR	2	N	M	S	NR	30.48	55.88	36.70	NA	2013-08-10	EM
FR	3	N	M	S	NA	40.64	104.14	44.37	0	2013-08-10	Chick
FR	4	N	M	S	NA	30.48	182.88	45.66	NA	2013-08-10	EM
FR	5	N	M	S	NA	24.765	164.465	27.03	NA	2013-08-10	EM
FR	6	N	M	NS	NR	63.5	60.96	11.79	NA	2013-08-10	EM
FR	6A	N	M	S	NR	40.64	97.79	24.59	NA	2013-08-10	EM
FR	6B	N	M	S	NR	35.56	30.48	19.28	1	2013-08-10	Chick
FR	6C	N	M	S	NR	22.225	54.61	13.01	NA	2013-08-10	EM
FR	6D	N	M	NS	R	25.4	54.61	18.72	NA	2013-08-10	EM
FR	6E	N	M	S	R	26.67	100.33	19.02	NA	2013-08-10	EM
FR	6F	N	M	S	R	27.94	74.93	20.76	NA	2013-08-10	EM
FR	7	N	M	S	R	12.7	81.28	26.47	0	2013-08-10	Chick

FR	7A	N	M	NS	R	31.75	129.54	34.41	0	2013-08-10	EM
FR	7A1	N	M	NS	R	27.94	127	27.42	NA	2013-08-10	EM
FR	7B	N	M	NS	NR	25.4	76.2	20.50	NA	2013-08-10	EM
FR	8	N	M	S	NR	15.24	86.36	23.60	0	2013-08-10	Chick
FR	8A	N	M	NS	NR	33.02	58.42	24.38	NA	2013-08-10	EM
FR	9	N	M	S	R	31.75	74.93	20.89	NA	2013-08-10	EM
FR	10	N	M	S	R	12.7	83.82	49.00	2	2013-08-10	Unknown
FR	10A	N	M	S	R	16.51	63.5	48.47	2	2013-08-10	Chick
FR	10B	N	M	S	NA	17.78	128.27	48.47	2	2013-08-10	Chick
FR	11	N	M	S	NR	19.05	91.44	22.90	0	2013-08-10	Chick
FR	11A	N	M	S	NR	25.4	63.5	30.64	NA	2013-08-10	EM
FR	11B	N	M	S	NR	30.48	101.6	15.63	NA	2013-08-10	EM
FR	11C	N	M	S	NR	17.78	52.07	13.65	0	2013-08-10	EM
FR	12	N	M	S	NR	25.4	68.58	9.52	NA	2013-08-10	EM
FR	13	N	M	S	NR	20.32	123.19	12.48	NA	2013-08-10	EM
FR	13A	N	M	S	R	27.94	72.39	13.79	NA	2013-08-10	EM
FR	14	N	M	NS	NR	21.59	71.12	43.15	NA	2013-08-10	EM
FR	14A	N	M	NS	NR	15.24	53.34	32.96	NA	2013-08-10	EM
FR	15	N	M	S	NR	22.86	58.42	14.87	NA	2013-08-10	EM
FR	16	N	M	S	NR	48.26	78.74	18.56	NA	2013-08-10	EM
FR	16A	N	M	S	NR	45.72	87.63	17.33	0	2013-08-10	RatPredation
FR	16B	N	M	S	NR	17.78	38.1	20.28	NA	2013-08-10	EM

FR	17	N	M	S	R	45.72	91.44	35.40	0	2013-08-10	Predation
FR	18	N	M	S	R	10.16	55.88	27.71	3	2013-08-10	Chick
FR	19	N	M	S	NR	29.21	91.44	27.71	NA	2013-08-10	EM
FR	20	N	M	S	R	39.37	127	27.71	2	2013-08-10	Chick
FR	21	N	M	S	R	29.21	50.8	27.15	2	2013-08-10	Chick
FR	22	N	M	S	NR	27.94	86.36	34.33	1	2013-08-10	Chick
FR	22A	N	M	S	NR	19.05	71.12	15.83	NA	2013-08-10	EM
FR	23	N	M	S	R	22.86	66.04	13.52	NA	2013-08-10	EM
FR	24	N	M	S	R	22.86	60.96	14.30	NA	2013-08-10	EM
FR	24A	N	M	S	NA	41.91	114.3	23.07	NA	2013-08-10	EM
FR	24B	N	M	S	NR	22.86	181.61	31.91	NA	2013-08-10	EM
FR	24C	N	M	S	R	34.29	76.2	15.08	0	2013-08-10	EM
FR	24D	N	M	S	R	17.78	71.12	23.93	0	2013-08-10	EM
FR	24E	N	M	S	NR	17.78	60.96	5.68	0	2013-08-10	Chick
FR	25	N	M	S	R	27.94	113.03	39.05	0	2013-08-10	Chick
GI	1	A	I	S	NR	25.4	76.2	NA	2	2013-08-16	EM
GI	2	A	I	S	R	20.32	76.2	NA	2	2013-08-16	Chick
GI	3	A	I	S	R	15.24	67.31	NA	2	2013-08-16	Chick
GI	4	A	I	S	NR	19.05	67.31	NA	0	2013-08-16	Chick
GI	5	N	I	S	NR	19.05	40.64	27.70	0	2013-08-16	Chick
HR	265	N	I	S	R	30.48	58.42	38.60	1	2013-08-16	EM
HR	263	N	I	S	R	17.78	55.88	39.92	NA	2013-08-16	EM

HR	262	A	I	S	NR	12.7	78.74	39.92	1	2013-08-16	Chick
HR	205	N	I	S	NR	25.4	69.85	29.49	1	2013-08-16	EM
HR	1	N	I	S	R	20.32	48.26	37.40	NA	2013-08-16	EM
HR	268	N	I	S	NR	22.86	59.69	24.57	2	2013-08-16	EM
HR	269A	N	I	S	R	38.1	114.3	24.20	2	2013-08-16	EM
HR	269	A	I	S	R	27.94	133.35	28.19	NA	2013-08-16	EM
HR	270	A	I	S	NR	17.78	68.58	28.77	0	2013-08-16	Chick
HR	271	A	I	S	R	21.59	71.12	24.84	0	2013-08-16	Chick
HR	273	A	I	S	NR	13.97	66.04	22.35	1	2013-08-16	Chick
HR	274	A	I	S	R	10.16	59.69	27.59	1	2013-08-16	EM
HR	283	A	I	S	NR	11.43	63.5	29.53	NA	2013-08-16	EM
HR	282	A	I	S	NR	10.16	63.5	21.84	1	2013-08-16	EM
HR	279	N	I	S	R	27.94	60.96	19.82	NA	2013-08-16	EM
HR	1A	N	I	S	R	33.02	78.74	24.04	1	2013-08-16	EM
HR	1B	N	I	S	NR	20.32	40.64	25.48	1	2013-08-16	Chick
LI	1	A	I	S	R	10.16	55.88	NA	1	2013-07-26	Chick
LI	2	A	I	S	R	10.16	71.12	NA	1	2013-07-26	Chick
LI	3	A	I	S	NR	7.62	58.42	NA	NA	2013-07-26	Adult
LR	16	A	I	S	NR	13.97	32.08	6.67	2	2013-07-30	Chick
LR	14	A	I	S	NA	12.7	147.32	6.67	NA	2013-07-30	Adult
LR	12	A	I	S	NR	12.7	203.2	6.51	3	2013-07-30	Chick
LR	1	N	I	S	NA	15.875	115.57	9.05	0	2013-07-30	Fledged

LR	19	A	I	S	NA	15.24	190.5	NA	0	2013-07-30	Chick
LR	5	N	I	S	NA	17.78	76.2	NA	0	2013-07-30	Chick
LR	15	N	I	S	NA	20.32	71.12	NA	NA	2013-07-30	EM
LR	17	N	I	S	NR	13.97	63.5	NA	0	2013-07-30	Chick
LR	6	A	I	S	NA	12.7	111.76	NA	NA	2013-07-30	EM
LR	F1	N	I	S	NA	45.72	365.76	NA	NA	2013-07-30	Chick
LR	18	N	I	S	NA	20.32	63.5	NA	NA	2013-07-30	Fledged
LR	13A	N	I	S	NR	12.7	55.88	10.93	NA	2013-07-30	EM
LR	9	N	I	S	NR	25.4	212.09	6.91	1	2013-07-30	Chick
LR	2	N	I	S	R	27.94	101.6	16.44	NA	2013-07-30	EM
LR	3	N	I	S	NA	25.4	93.98		NA	2013-07-30	EM
NI	386	A	I	S	R	15.24	76.2	22.22	NA	2013-08-20	EM
NI	387	A	I	S	R	16.51	81.28	34.87	3	2013-08-20	Chick
NI	388	A	I	S	NR	11.43	67.31	36.91	4	2013-08-20	Chick
NI	383	A	I	S	NR	8.89	57.15	27.32	3	2013-08-20	Chick
NI	384	A	I	S	NR	10.16	57.15	20.84	4	2013-08-20	CrowPredation
NI	1	A	I	S	R	10.16	55.88	33.59	2	2013-08-20	Chick
NI	2	A	I	S	R	17.78	72.39	NA	0	2013-08-20	Chick
NI	284	A	I	S	R	24.13	83.82	19.60	NA	2013-08-20	Unknown
NI	286	A	I	S	NR	12.7	63.5	20.41	NA	2013-08-20	EM
NI	287	A	I	S	R	22.86	80.01	32.29	0	2013-08-20	Chick
NI	300	A	I	S	R	22.86	66.04	32.88	0	2013-08-20	Unknown

NI	391	A	I	S	R	19.05	69.85	11.11	0	2013-08-20	Fledged
NI	392	A	I	S	NR	15.24	90.17	11.04	0	2013-08-20	Chick
NI	393	A	I	S	R	20.32	71.12	31.40	1	2013-08-20	Chick
NI	3	A	I	S	R	25.4	71.12	52.67	2	2013-08-20	Egg
NI	4	A	I	S	R	17.78	73.66	51.53	NA	2013-08-20	EM
NI	5	A	I	S	NR	12.7	48.26	45.50	1	2013-08-20	Chick
NI	394	A	I	S	R	15.24	67.31	0.00	0	2013-08-20	Fledged
NI	395	A	I	S	NR	12.7	66.04	0.00	1	2013-08-20	Chick
NI	396	A	I	S	NR	15.24	66.04	0.00	1	2013-08-20	Fledged
NI	397	A	I	S	NR	15.24	71.12	31.45	0	2013-08-20	Fledged
NI	288	A	I	S	R	10.16	67.31	3.71	0	2013-08-20	Fledged
NI	289	A	I	S	R	22.86	63.5	NA	NA	2013-08-20	Chick
NI	398	A	I	S	NR	20.32	68.58	4.95	NA	2013-08-20	EM
NI	299	A	I	S	NR	17.78	67.31	31.45	1	2013-08-20	Fledged
NI	400	A	I	S	NR	17.78	78.74	31.45	NA	2013-08-20	EM
NI	51	N	I	S	NR	16.51	88.9	31.45	2	2013-08-20	Fledged
NI	399	A	I	S	NR	17.78	83.82	31.45	1	2013-08-20	Chick
NI	298	A	I	S	NR	17.78	76.2	31.45	NA	2013-08-20	EM
NI	6	A	I	S	NR	13.97	64.77	25.23	0	2013-08-20	Chick
NI	296	A	I	S	NR	19.05	60.96	31.45	1	2013-08-20	Chick
NI	297	A	I	S	NR	15.24	71.12	31.45	1	2013-08-20	Fledged
NI	7	A	I	S	NR	12.7	64.77	16.21	0	2013-08-20	Chick

NI	8	A	I	S	R	13.97	71.12	29.64	NA	2013-08-20	EM
NI	9	N	I	NS	R	55.88	113.03	13.67	0	2013-08-20	EM
NI	3A	A	I	S	R	15.24	77.47	16.33	0	2013-08-20	Chick
NI	376	N	I	S	NR	15.24	121.92	37.87	0	2013-08-20	Chick
NI	377	N	I	S	R	30.48	127	36.23	0	2013-08-20	Chick
NI	292	N	I	S	R	31.75	92.71	14.86	0	2013-08-20	Chick
NI	293	N	I	S	R	21.59	77.47	16.16	1	2013-08-20	Chick
NI	378	N	I	S	R	54.61	269.24	36.23	0	2013-08-20	Chick
NI	CLIFF	N	I	S	NR	19.05	50.8	31.45	1	2013-08-20	EM
NI	131	A	I	S	NR	15.24	50.8	23.46	1	2013-08-20	Chick
NI	132	A	I	S	NR	17.78	62.23	26.00	NA	2013-08-20	EM
NI	125	A	I	S	NR	19.05	66.04	7.44	0	2013-08-20	Chick
NI	133	A	I	S	NR	13.97	60.96	23.28	0	2013-08-20	Chick
NI	134	A	I	S	NR	13.547	57.15	23.28	0	2013-08-20	Fledged
NI	137	A	I	S	NR	17.78	63.5	23.28	NA	2013-08-20	EM
NI	135	A	I	S	NR	16.51	57.15	23.28	NA	2013-08-20	EM
NI	138	A	I	S	R	16.51	50.8	23.28	0	2013-08-20	EM
NI	139	A	I	NS	R	21.59	68.58	23.28	0	2013-08-20	EM
NI	136	A	I	S	NR	15.24	53.34	28.50	NA	2013-08-20	EM
NI	127	A	I	S	R	24.13	63.5	28.39	0	2013-08-20	Chick
NI	128	A	I	S	R	25.4	68.58	19.90	0	2013-08-20	Fledged
NI	389	A	I	S	NR	17.78	74.93	33.09	1	2013-08-20	Chick

NI	389A	A	I	S	NR	16.51	69.85	31.98	1	2013-08-20	Chick
NI	389B	N	I	S	R	25.4	63.5	22.88	0	2013-08-20	Chick
PI	1	A	I	S	R	11.43	57.15	NA	1	2013-07-08	Chick
PI	2	A	I	S	R	10.16	59.69	NA	1	2013-07-08	Chick
RI	1	A	I	S	NR	19.05	55.88	NA	1	2013-08-16	Fledged
RI	2	A	I	S	R	22.86	64.77	NA	1	2013-08-16	Fledged
RI	3	A	I	S	R	16.51	52.07	NA	0	2013-08-16	Fledged
RIs	1	N	I	S	R	27.94	67.31	NA	0	2013-07-08	RatPredation
SB	1	A	M	S	R	16.51	67.31	30.00	0	2013-08-21	Chick
SB	2	A	M	S	NR	12.7	53.34	26.40	NA	2013-08-21	EM
SB	3	A	M	S	NR	11.43	59.69	26.89	NA	2013-08-21	EM
SB	4	A	M	S	R	11.43	63.5	28.27	0	2013-08-21	Fledged
SB	15	N	M	S	NR	22.86	83.82	26.12	0	2013-08-21	Chick
SB	20	N	M	S	NR	60.96	116.84	33.85	0	2013-08-21	Fledged
SB	19	N	M	S	NR	10.16	109.22	21.89	NA	2013-08-21	EM
SB	16	N	M	S	NR	10.16	68.58	19.30	0	2013-08-21	Chick
SB	21	N	M	S	NR	17.78	86.36	20.89	0	2013-08-21	Chick
SB	22A	N	M	S	R	12.7	58.42	15.05	0	2013-08-21	Fledged
SB	22	N	M	S	NR	20.32	76.2	32.03	0	2013-08-21	Fledged
SB	23	N	M	S	NR	40.64	132.08	22.45	NA	2013-08-21	EM
SB	24	N	M	S	NR	10.16	73.66	16.68	NA	2013-08-21	EM
SB	25	N	M	S	NA	22.86	127	20.53	1	2013-08-21	Fledged

SB	25A	N	M	S	NR	15.24	63.5	22.09	1	2013-08-21	Fledged
SB	26	N	M	S	NR	20.32	120.65	35.39	0	2013-08-21	Fledged
SB	27	N	M	S	NR	13.97	72.39	35.94	NA	2013-08-21	EM
SB	28	N	M	S	R	17.78	85.09	35.23	0	2013-08-21	EM
SB	29	N	M	S	NR	16.51	115.57	31.42	0	2013-08-21	Fledged
SB	17	N	M	S	R	21.59	78.74	27.71	0	2013-08-21	Fledged
SB	18	N	M	S	NR	12.7	109.22	28.43	0	2013-08-21	Fledged
SB	30	N	M	NS	NR	15.24	69.85	19.23	NA	2013-08-21	EM
SB	31	N	M	S	NR	11.43	93.98	23.35	0	2013-08-21	Fledged
SB	31A	N	M	NS	NR	22.86	63.5	20.69	NA	2013-08-21	EM
SB	32	A	M	S	NR	10.16	78.74	20.71	0	2013-08-21	Fledged
SI	344	N	I	S	R	25.4	101.6	9.89	NA	2013-08-16	EM
SI	311	N	I	S	R	58.42	87.63	30.33	NA	2013-08-16	EM
SI	361	N	I	S	NR	53.34	143.51	38.50	NA	2013-08-16	EM
SI	312	N	I	S	NR	30.48	140.97	38.50	NA	2013-08-16	EM
SI	313	N	I	S	R	83.82	96.52	31.83	NA	2013-08-16	EM
SI	314	N	I	S	NR	39.37	200.66	31.92	NA	2013-08-16	EM
SI	316	N	I	S	NR	33.02	76.2	31.92	NA	2013-08-16	EM
SI	317	N	I	S	NR	10.16	114.3	39.12	2	2013-08-16	Chick
SI	355	N	I	S	R	12.7	116.84	30.33	NA	2013-08-16	EM
SI	320	N	I	S	R	12.7	60.96	39.99	NA	2013-08-16	Adult
SI	341	N	I	S	R	21.59	48.26	30.73	1	2013-08-16	Adult

SI	342A	N	I	S	NA	11.43	119.38	NA	NA	2013-08-16	EM
SI	342B	N	I	S	NA	15.24	45.72	NA	NA	2013-08-16	Chick
SI	345	N	I	S	NA	33.02	81.28	NA	2	2013-08-16	Adult
SI	345A	N	I	S	NA	25.4	104.14	NA	2	2013-08-16	EM
SI	345B	N	I	S	NA	21.59	59.69	NA	NA	2013-08-16	Chick
SI	345C	N	I	S	NA	17.78	78.74		NA	2013-08-16	Chick
SI	304	N	I	S	R	16.51	111.76	10.16	NA	2013-08-16	Adult
SI	404	N	I	S	R	55.88	121.92	7.72	NA	2013-08-16	EM
SI	303	N	I	NS	R	35.56	69.85	10.43	0	2013-08-16	EM
SI	306	N	I	S	R	12.7	72.39	7.37	NA	2013-08-16	EM
SI	307QUA	N	I	S	R	20.32	78.74	10.63	0	2013-08-16	Chick
SI	366	A	I	S	R	15.24	86.36	49.85	NA	2013-08-16	EM
SI	367	A	I	S	NR	19.05	83.82	52.04	0	2013-08-16	Unknown
SI	368	A	I	S	R	12.7	93.98	52.60	0	2013-08-16	Unknown
SI	369	A	I	S	NR	15.24	82.55	47.31	1	2013-08-16	Unknown
SI	370	A	I	S	NR	15.24	78.74	41.23	1	2013-08-16	Chick
SI	371	A	I	S	NR	16.51	96.52	37.89	1	2013-08-16	Chick
SI	372	A	I	S	NR	16.51	81.28	43.57	1	2013-08-16	Chick
SP	1	N	M	S	R	20.32	57.15	29.53	0	2013-08-10	Chick
SP	1A	N	M	S	R	30.48	162.56	33.80	NA	2013-08-10	EM
SP	2	N	M	S	NR	26.67	236.22	38.56	NA	2013-08-10	EM
SP	3	N	M	S	NR	25.4	236.22	37.87	NA	2013-08-10	Adult

SP	4	N	M	S	NR	20.32	203.2	30.77	1	2013-08-10	Chick
SP	5	N	M	S	NR	30.48	193.04	46.33	2	2013-08-10	Chick
SP	6	N	M	S	NR	20.32	251.46	55.77	1	2013-08-10	Chick
SP	7	N	M	S	R	35.56	128	NA	0	2013-08-10	Chick
SP	7A	N	M	S	NR	24.13	218.44	36.73	0	2013-08-10	Chick
SP	8	N	M	S	NR	22.86	55.88	26.65	NA	2013-08-10	EM
SP	9	A	M	S	NR	17.78	90.17	31.81	NA	2013-08-10	EM
SP	10	N	M	S	R	15.24	152.4	12.83	NA	2013-08-10	EM
SP	11	N	M	S	R	13.97	147	11.43	1	2013-08-10	Chick
SP	12	N	M	S	NR	17.78	128.27	13.86	1	2013-08-10	Chick
SP	13	N	M	NS	NR	40.64	76.2	33.45	NA	2013-08-10	EM
SP	14	N	M	NS	NR	40.64	86.36	18.49	NA	2013-08-10	EM
SP	15	N	M	S	NA	11.43	162.56	32.63	NA	2013-08-10	EM
SP	16	N	M	NS	NR	99.06	105.41	23.28	NA	2013-08-10	EM
SP	17	N	M	NS	NR	31.75	73.66	16.05	NA	2013-08-10	EM
SP	18	N	M	S	NR	16.51	114.3	26.06	0	2013-08-10	Chick

Table 1-A1. Full model selection results for testing hypotheses about the effects of nest-site characteristics and breeding season on Bermudian White-tailed Tropicbird clutch survival.

Model	K[a]	Model Likelihood[b]	AICc[c]	ΔAIC[d]	*w*[e]	Dev[f]
Rubble + Cavity depth + EH	4	1	855.6	0	0.9	847.6
Global Model	10	0.02	863.2	7.6	0	843.2
Cavity type + Rubble + Cavity depth	4	0.02	863.9	8.3	0	855.9
Cavity type + Cavity depth + EH	4	0.01	864.2	8.6	0	856.2
Location+ Cavity depth + EH	4	0.01	864.4	8.8	0	856.4
Cavity type + Location + Cavity depth + EH	5	0.01	866	10.5	0	856
Location+ Rubble + Cavity depth	4	0	867.7	12.1	0	859.7
Cavity type + Cavity depth	3	0	873	17.4	0	867
2015 + Cavity depth	3	0	873.5	17.9	0	867.5
Cavity type + Rubble + EH	4	0	873.7	18.1	0	865.7
Cavity depth	2	0	874.1	18.5	0	870.1
2014 + Cavity depth	3	0	874.6	19	0	868.6
Cavity depth + Coastal slope	3	0	875.2	19.6	0	869.2
Cavity type + Cavity depth	3	0	875.8	20.2	0	869.8
Location + Cavity depth	3	0	876.1	20.5	0	870.1
Rubble	2	0	876.2	20.6	0	872.2
EH + Coastal slope	3	0	881.2	25.6	0	875.2
EH	2	0	883.1	27.5	0	879.1
Coastal slope	2	0	885.9	30.3	0	881.9
B0	1	0	887.4	31.8	0	885.4
Cavity type + Location	3	0	887.5	31.9	0	881.5
Neighbors + Coastal slope	3	0	887.5	31.9	0	881.5
Location	2	0	887.7	32.1	0	883.7
2014	2	0	887.9	32.3	0	883.9
Neighbors	2	0	888.2	32.6	0	884.2
Cavity type	2	0	888.2	32.6	0	884.2
2014 + 2015	3	0	888.5	32.9	0	882.5

a Number of parameter estimates
b Model likelihood
c Akaike's information criterion
d. Difference in AICc values of the current and top-ranked
e. Weight of evidence supporting
f. Deviance not explained by each model

Table 2-A1. Full model selection results for testing hypotheses about the effects of nest-site characteristics and breeding season on Bermudian White-tailed Tropicbird nestling survival.

Model	K[a]	Model Likelihood[b]	AIC[c]	ΔAIC[d]	*w*[e]	Dev[f]
2014 + 2015 + Time + Nestling age	5	1.00	305.1	0.0	0.9	295.1
2014 + 2015 + Nestling age	4	0.03	312.0	6.9	0.0	304.0
2015 + Time + Nestling age	4	0.01	313.7	8.6	0.0	305.7
Global Model	11	0.01	314.0	8.9	0.0	292.0
2015 + Nestling age	3	0.00	318.1	13.0	0.0	312.1
Time + Nestling age	3	0.00	322.3	17.2	0.0	316.3
Caity depth +Time + Nestling age	4	0.00	323.5	18.4	0.0	315.5
2014 +Time + Nestling age	4	0.00	324.2	19.2	0.0	316.2
Nestling age	2	0.00	325.1	20.0	0.0	321.1
Cavity type + Location + Time + Nestling age	5	0.00	325.2	20.1	0.0	315.2
Cavity depth + Nestling age	3	0.00	326.0	20.9	0.0	320.0
2014 + Nestling age	3	0.00	326.9	21.8	0.0	320.9
Location + Nestling age	3	0.00	327.1	22.0	0.0	321.1
Nest Type + Cavity depth + Nestling age	4	0.00	327.6	22.5	0.0	319.6
2014 + 2015 + Time	4	0.00	384.4	79.3	0.0	376.4
Time	2	0.00	391.7	86.6	0.0	387.7
2015	2	0.00	402.2	97.1	0.0	398.2
B0	1	0.00	408.8	103.7	0.0	406.8
Neighbors	2	0.00	409.1	104.1	0.0	405.1
Nest type	2	0.00	409.6	104.5	0.0	405.6
Entrance height	2	0.00	410.5	105.4	0.0	406.5
Coastal slope	2	0.00	410.6	105.5	0.0	406.6
2014	2	0.00	410.6	105.5	0.0	406.6
Coastal slope + Neighbors	3	0.00	411.1	106.1	0.0	405.1
Nest type + Location + Cavity depth + EH	5	0.00	414.4	109.3	0.0	404.4

a Number of parameter estimates
b Model likelihood
c Akaike's information criterion
d. Difference in AICc values of the current and top-ranked
e. Weight of evidence supporting
f. Deviance not explained by each model

Plate 1-A1. White-tailed Tropicbird adult with an egg inside a natural nest-cavity at Cooper's Island, Bermuda. Photo by Miguel Mejías in 2015.

Plate 2-A1. White-tailed Tropicbird hatchling approximately 3-4 days on Nonsuch Island, Bermuda. Note that eyes are closed and head usually held with bill pointed up. Egg tooth on bill evident at this stage. Photo by Miguel Mejías in 2013.

Plate 3-A1. White-tailed Tropicbird early downy chick approximately 1-2 weeks old inside a natural nest-cavity in Bermuda. Note that the eyes are open and the bill has turned brighter yellow and is larger than chick in previous plate. Late downy chick (as mentioned in appendix table) would have the same appearance as an early downy chick but is slightly larger in body size. Photo by Miguel Mejías in 2014.

Plate 4-A1. White-tailed Tropicbird early-scapular chick that is approximately 3 weeks old from an artificial cavity at Bay House, Bermuda. The chick is much larger than the chick in the previous plate especially the head, which causes the bird to take on a more elongated appearance. The black scapular feathers have started to emerge. This bird is 1/4 fledged. Photo by Miguel Mejías in 2015.

Plate 5-A1. White-tailed Tropicbird middle scapular chick approximately 4 weeks old from one of the Castle Harbor Islands, Bermuda. The chick is much larger than the chick in the previous plate, with more flight feathers emerging along the scapulars and wings. This bird is 1/3 fledged. Photo by Miguel Mejías in 2012.

Plate 6-A1. White-tailed Tropicbird half-fledged chick 5 weeks old from an unknown nest-cavity in Bermuda. The breast, wings and back are covered in fledgling feathers while the head, neck and tail are covered in downy feathers. At this stage nestlings can assume an upright position. This bird is 1/2 fledged. Photo by Miguel Mejías in 2012.

Plate 7-A1. White-tailed Tropicbird 2/3 fledged chick approximately 6-7 weeks old on Southampton Island, Bermuda. The downy feathers have molted from the forehead region, giving the chick a “lion’s mane” appearance. The downy feathers are also moulted from the main body. The chick has almost reached its full body size. Photo by Miguel Mejías in 2014.

Plate 8-A1. White-tailed Tropicbird 3/4 fledged chick approximately 8-9 weeks old inside an unknown nest-cavity in Bermuda. The chick has lost most of its down feathers from its body. The wingtips do not reach the base of the tail feathers. Photo by Miguel Mejías in 2012.

Plate 9-A1. White-tailed Tropicbird fully fledged chick approximately 10-13 weeks old at Ferry Reach, Bermuda. The chick is completely down free and fully grown. The tips of flight feathers touch the base of the tail feathers and cross when folded. Photo by Miguel Mejías in 2016.

Appendix 2- Images and data pertaining to the non-breeding distribution and at-sea behaviour of adult White-tailed Tropicbirds from Bermuda.

Plate 1-A2. The tarsi of a breeding White-tailed Tropicbird fitted with a single Migrate Tec Intigeo C-65 (1 gram) geolocator (< 0.5% of adult White-tailed Tropicbird's body mass) secured onto a plastic darvick band with a combination of marine epoxy and a small zip tie. B: A breeding White-tailed Tropicbird carrying a single Migrate Tec Intigeo C-65 on its tarsi while incubating.

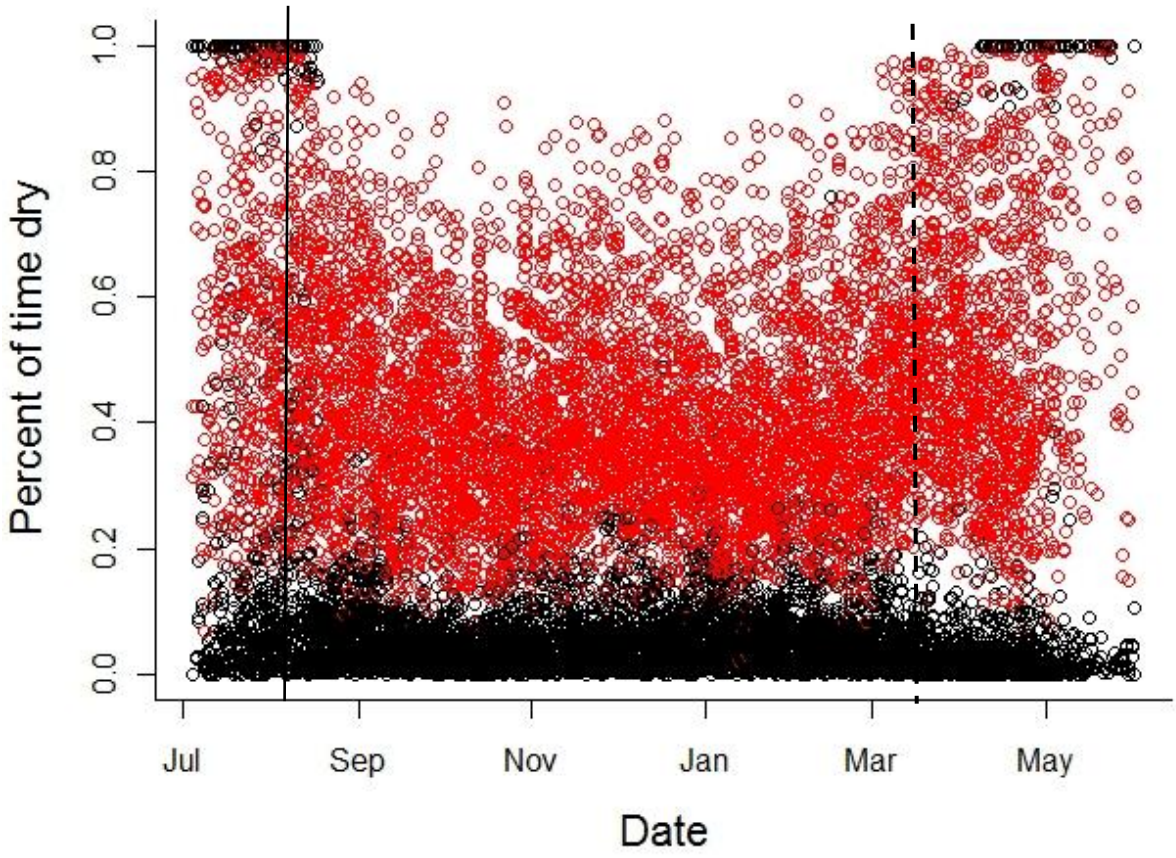

Figure 1-A2. Total time 25 tagged White-tailed Tropicbirds were dry during day (red circles) and night (dark circles) periods during the breeding and non-breeding period. The approximate start and end of the non-breeding period are denoted with a solid and dashed line respectively. Total percent time dry during day and night periods declined during the non-breeding period and steadily increased during the following breeding period.